INTRASPECIFIC VARIATION AND RELATIONSHIPS OF SOME LOWER ORDOVICIAN SPECIES OF THE DICHOGRAPTID, *CLONOGRAPTUS*

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ABSTRACT. The genus *Clonograptus* is redefined as a form genus consisting of one phylogenetically based subgenus, *Clonograptus s.s.*, and additional species of uncertain relationships. *Clonograptus* is transferred from the Anisograptidae to the Dichograptidae, since bithecae are absent along the stipes in the type species. *Temnograptus*, *Herrmannograptus*, *Anthograptus*, and ?*Calamograptus* are considered synonyms of *Clonograptus s.s.*, based on a large fauna of '*Temnograptus*' *multiplex* that shows extreme variation, especially in stipe length. This variation indicates that the diagnostic characters of these genera are not tenable. It also suggests that 'stipe order' is an artificial concept in clonograptids, with stipe length being instead an expression of functional morphology. The *C. (C.) multiplex* fauna is in part very well preserved and details of proximal morphology are described from relief specimens. A closely related but slightly older species, *C. (C.) sp. aff. C. multiplex*, exhibits features transitional between the families Anisograptidae and Dichograptidae, necessitating a refinement of their diagnoses. In Dichograptidae we allow a sicular bitheca, and/or stipes with a triad budding mechanism but without bithecae. As a consequence, all 'clonograptids' with bithecae along the stipes must be referred to another, anisograptid, genus. The morphology and preservation of clonograptids, and the resulting constraints on the use of statistical methods, are extensively discussed.

THE original description by Nicholson (1868) of '*Dichograpsus*' *multiplex*, from the Middle Skiddaw Slates, was based on two badly preserved specimens that showed no fine details of the rhabdosome. Recently, more than 100 specimens of *Clonograptus* (*Clonograptus*) *multiplex*, some of them in relief, have been collected from Mount Hunneberg in Västergötland, west-central Sweden. The strata belong to the post-Tremadoc Hunneberg substage, as defined by Tjernvik (1956). The fauna shows an extreme intraspecific variation and irregularity of branching intervals. The relatively small number of specimens available to earlier authors did not permit an overview of this variation, and hence a number of specific and generic names have been introduced (see e.g. Törnquist 1904; Monsen 1937), as well as such informal identifications as 'undetermined irregular Dichograptidae' (Törnquist 1904). Measurements on the material at hand have shown no discontinuities in any significant parameters.

In addition to *C. multiplex*, a number of closely related and approximately contemporaneous *Clonograptus* species, including the type species, are described (some of which are also found at Mt. Hunneberg). *Clonograptus s.s.* is redefined, and is, for practical reasons, referred to as a subgenus of the form genus *Clonograptus s.l.*, following the model introduced by Cooper and Fortey (1982) for *Tetragraptus* and *Didymograptus*. *Clonograptus s.s.* is characterized by a combination of proximal development, branching pattern, and thecal shape. The thecal shape is constant throughout the rhabdosome, and no bithecae are found along the stipes. Thus, some Tremadoc species, and forms with narrowing of the stipes, indicating morphological changes, are excluded from the subgenus, as are provisionally a number of species whose thecal characters are not known.

Species of *Clonograptus s.s.* first appear in the uppermost Tremadoc, but are mostly reported to be associated with *Tetragraptus approximatus*. Geographically they are known from Canada (e.g. J. Hall 1858, 1865; Kindle and Whittington 1958; Jackson 1974), the USA (e.g. J. Hall 1861; Berry 1960; Braithwaite 1976), Argentina (Aceñolaza *et al.* 1976), Australia (e.g. Pritchard 1895), New Zealand (Cooper 1979, pl. 1, fig. f; pl. 2, fig. f), China (Li 1983, pl. 1, fig. 1; Xiao 1987, pl. 2,

fig. 1), Spain (Gutierrez Marco 1986, pl. 10, figs. 1, 3, 6, 7), France (Thoral 1935), Czechoslovakia (Kraft and Mergl 1979), Great Britain (e.g. Nicholson 1868; Jackson 1979), Greenland (Bjerreskov and Poulsen 1973), and Scandinavia (e.g. Herrmann 1882; Törnquist 1904). '*Clonograptus?*', '*Temnograptus*', and '*Herrmannograptus*' have also been reported from the Lower Arenig of Poland (Modliński, pers. comm.). In addition, a number of *Clonograptus s.l.* species from different regions may turn out to belong to *Clonograptus s.s.* when studied in detail.

In this revision the suprageneric taxonomy of Fortey and Cooper (1986) is used, in slightly emended form.

MORPHOLOGY, FUNCTION, AND PRESERVATION

The clonograptids have several orders of branching and show great variation between specimens. Some of this variation is obviously due more to preservation than original morphology. As preservational variation is an important but often neglected factor in graptolite identification, we have chosen here to stress these aspects.

Morphology

Due to the shape of the rhabdosome, mature specimens of *Clonograptus* are almost invariably preserved horizontally, i.e. in dorso-ventral view with thecal apertures pointing upwards or downwards, thus obscuring important characters needed for specific, and also higher rank, distinctions (e.g. the presence or absence of bithecae). The proximal part of a graptolite rhabdosome is of prime phylogenetic importance (Cooper and Fortey 1982, p. 181; Fortey and Cooper 1986, table 1), and is on rare occasions seen in profile view in immature *Clonograptus* specimens with a maximum of four stipes (cf. Pl. 83, fig. 1). Evidently the identity of such a specimen by itself might be questioned: could it not be a *Tetragraptus*? For this reason we have relied on specimens from apparently monotypical associations, consisting of rhabdosomes of different sizes.

According to Fortey and Cooper (1986, table 1) the next most phylogenetically significant characters of the rhabdosome relate to the branching pattern, such as distances between dichotomies and angles between daughter stipes. In many multiramous genera the position of dichotomies is fixed, or nearly so. In *Clonograptus*, however, only the first dichotomy is fixed and the second one is, in most species, consecutive. The following dichotomies are unpredictable, although the average stipe length is to some extent diagnostic.

The form and elaboration of non-proximal thecae was assigned the least phylogenetic importance by Cooper and Fortey (1986). In *Clonograptus s.s.* the thecae are simple tubes, possibly slightly expanded towards the aperture. Morphological changes along the stipes are not known in *Clonograptus s.s.* Only the most distal two or three thecae were apparently growing at any one time, so stipe width and thecal inclination should not vary between immature and mature specimens. Distal *Clonograptus* stipes are often twisted, presenting a more or less perfect profile view, in which case the number of thecae in 10 mm can be counted. A full profile view is needed for the correct measurement of other thecal parameters. However, details are often obscured by the addition of cortical tissue in mature specimens. The amount of cortical tissue varies considerably between otherwise very similar specimens, and we do not regard it as diagnostic at the species level.

Forms with bithecae were treated separately by Fortey and Cooper (1986) who referred them to the paraphyletic family Anisograptidae within the Graptoloidea. It is quite possible that a sicular bitheca and other primitive traits exist in some species of *Clonograptus s.s.*, as will be discussed below. In order not to split a natural group of taxa we have chosen to refer such forms also to the Dichograptidae. The recognition of bithecae in graptolites is only possible in high relief specimens, preferably in profile view. The same goes for the remnants of triad budding, found in some taxa with a sicular bitheca, where the (auto)thecae are seen to alternate (Pl. 83, fig. 7) even though bithecae are absent.

Morphological terms used in this paper accord mainly with Bulman (1970) and Cooper and Fortey

(1982, 1983). We use *first dichotomy* for the one giving rise to the two-stiped stage, '*trichotomy*' for two consecutive dichotomies in a stipe, and '*quadrichotomy*' for three consecutive dichotomies in a stipe. *Proximal part*, as used herein, includes first- and second-order stipes. The *sicular bitheca* originates from th1[1] about half way down the sicula; it is aligned with the sicula on its obverse side.

Functional morphology

Branching characteristics. In previous descriptions of species here referred to *Clonograptus s.s.* it is often stated that the angle of divergence decreases with each successive dichotomy. Our measurements indicate that this is not quite true. Untwisted branches of any *Clonograptus* species described below never show an initial angle of divergence less than 45–50°. To avoid overlap, the stipes may curve subsequently to adopt a more or less parallel orientation. The reason for this minimum angle could be either constructional constraints or interference in feeding between adjacent zooids. The second alternative is favoured here, since the distance between the first post-dichotomy pair of zooids is approximately the same as that between successive zooids (Pl. 83, fig. 2).

　　Another interpretation may be valid for the higher angles of divergence found at the second and third dichotomies, usually 90–100° and 60–80° respectively. The combination of very short first-order stipes (i.e. a tetragraptid proximal part) and a second dichotomy of just over 90° produces approximately equal spacing between all four stipes in the immature rhabdosome. This pattern of branching may result from a need to maintain a balance in the water column.

　　The irregular branching intervals in *Clonograptus* can also be explained as a functional adaptation. If all branches divided simultaneously, the resulting localized belt of overcrowding, would have diminished the feeding area for individual zooids in that region. Instead, the stipes of a rhabdosome are fairly evenly spaced, with dichotomies occurring when the distance between two adjacent stipes becomes unacceptably great; text-fig. 6A illustrates a good example of this – note the 'abnormally' long fourth-order stipe, which has obviously suppressed branching in order not to encroach on adjacent branches. This regularity of inter-stipe distances is seen more easily in *C. flexilis* than in *C. multiplex*, since the variation between specimens is much greater in the latter. It follows, therefore, that the order of a stipe in *Clonograptus* is an artificial concept, with branching position being a result of practical needs *not* inherent programming. Similar ideas were also proposed by Cooper (1985) for *C. trochograptoides*.

　　Fortey and Bell (1987) compared computer-generated models of multiramous graptolites with real colony shapes. They concluded that the factors controlling the shape of biradiate multiramous rhabdosomes were primarily genetic, but that inhibitory action between adjacent stipes might have suppressed stipe division to avoid overcrowding. Their conclusion as to why this suppression occurred agrees with ours: the optimal use of food resources. They also suggested (1987, p. 16) that responses to the 'apparent awareness of neighbouring stipes', which made distal stipes curve to keep an even distance between themselves, could have been either 'coordinated by way of information transmitted through the common canal' or were 'a direct response between neighbouring stipes'. We agree with their observation that crossing-over stipes are very rare, and that this indicates an approximately planar rhabdosome. The 'primary genetic programming' suggested by Fortey and Bell (1987) might have been less important in clonograptids than in other multiramous forms; see, for example, text-fig. 6B with its two very differently developed lower quadrants that were obviously adjusted to each other.

Bithecae. A sicular bitheca is present in at least *C. milesi* and probably also in the type species. The presence of a bithecal individual persists after the general disappearance of bithecae along the stipes. Its position between the sicula and the first theca could be used as an argument against its reproductive role (Kirk 1969, p. 291), unless the sicular individual was specialized for this purpose, rather than the thecal zooids. If, on the other hand, the sicular individual had the same function as all thecal zooids, it would seem more probable that the persistent bithecal individual had a function reminiscent of bryozoan avicularia or echinoderm pedicellariae, i.e. that of defence and removal of

parasites and settling larvae. This function was suggested by Kirk (1973, p. 5). The presence of parasites or epibionts would be most injurious to a young colony, particularly a floating one.

Preservation

Graptolite identification is often hampered by the different modes of compaction resulting from a variation of physical and chemical factors in the environment of deposition. One chemical factor is the content of carbonate. A lime-mud has little capacity for compaction, due to early cementation. Unless highly bituminous, a limestone also suggests an oxygenated environment, and a low sedimentation rate would have left the graptolites exposed on the sediment surface to suffer aerobic breakdown of their scleroproteinaceous skeletons (cf. Cooper and Fortey 1982, p. 162). A graptolite which originally settled in lime-mud may thus now be three-dimensionally preserved, but might at the same time show a brittle type of compaction. The types of deformation resulting from varying brittleness of the rhabdosome were studied by Williams *et al.* (1982).

Pyritization of graptolites, another diagenetic process that leads to full or partial three-dimensional preservation, was dependent on chemical factors. Berner (1984) discussed the environments which favour the production of pyrite. Under certain conditions, appreciable amounts of pyrite can form in oxidizing as well as reducing environments. In the former case, pyrite formation is favoured by a high sedimentation rate, and can only take place below the sediment surface; in the latter case, a low sedimentation rate is favourable and pyrite can then also form synsedimentarily, on the sediment surface. At least some of our graptolites from Mt. Hunneberg were pyritized under oxidizing conditions, since they occur in a bioturbated sediment. This indicates a rather high sedimentation rate for the *Clonograptus*-bearing strata, which consist of virtually non-calcareous grey to black shales. The darker beds are coloured by finely disseminated pyrite. Pyritized graptolites in bioturbated silty shales have also been found at Lévis, Quebec (e.g. text-fig. 5A).

The physical factors which most influence the type of preservation are grain-size and water content of the surface layer. A soft, water-soaked sediment allows vertical burial of thecae or even of whole rhabdosomes. The quadriserial phyllograptoids are good indicators of this. In originally soft sediments most rhabdosomes take up a ' + '-position, with their axes lying along the sediment surface; only a *very* soft sediment permitted a 'vertical' orientation to survive. On a firmer substrate, however, only the ' × '-position was stable. Rex (1986) has shown that sediment grain-size strongly influences the type of compaction. A tube-like fossil compressed in a mud-grade sediment increases in width, whereas burial in a sand-grade sediment will result in a decrease in width, possibly accompanied by the crumpling of rigid materials. The same mechanism might explain some of the differences observed between *C. flexilis* and *C. rigidus*. According to J. Hall (1865, pp. 103, 105), *C. rigidus* was always found in a coarser lithology than *C. flexilis* and usually has narrower stipes than the latter, a difference which may be in part preservational.

There have been various opinions expressed regarding the change in dimensions of graptolites upon compression. Rickards and Palmer (1977) assumed a marked increase in width in flattened specimens, whereas Williams *et al.* (1982) and Fortey (1983) found no significant lateral spreading. These contrasting results can partly be explained by the fact that these authors have studied graptolites with different thecal morphologies, preserved in different matrices.

The experiments of Williams *et al.* were conducted in an embedding medium which compacted to 55% of its original volume, in nature corresponding to a limestone; their graptolites were 'complicated' uniserials and biserials with elaborate thecae. Such graptolites had various strengthening walls in different directions and were thus likely to resist deformation. Any conclusions regarding the compaction of these forms are unlikely to be representative for dichograptids, with their simple-tube thecae (like our clonograptids), preserved in a shale matrix that may have been compressed to 10% of its original volume.

Rickards and Palmer (1977, pp. 60–62) discussed uniserial specimens with partly straight and partly climacograptid thecae, preserved in a 'muddy siltstone' (1977, p. 66). Their reasoning was a theoretical interpretation of details seen in the rhabdosomes, and they concluded that in graptolites

with simple thecae the interthecal septum was bent ventrally upon compression, giving a lateral spread. The details discussed are often seen in well-preserved specimens of *C. multiplex* from Hunneberg, as well as in other dichograptids we have studied.

Fortey (1983, p. 123), on the other hand, stated that for several species from the early Ordovician of Spitsbergen he had been 'unable to measure any difference between flattened and unflattened specimens', if seen in profile view. Since he compared flattened and isolated material, the lithology probably had a high carbonate content.
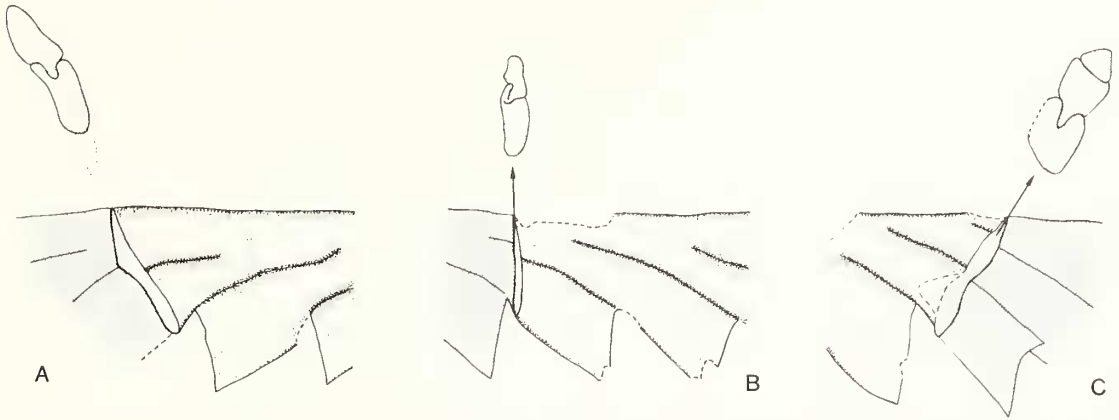
TEXT-FIG. 1. Three broken stipe fragments of *Didymograptus* cf. *bifidus* from black shale at the 79·33–79·38 m level of the Krapperup core, north-west Scania, Sweden. The specimens are pyritized with preserved periderm, and the cross-sections (top of figure) show the response of the graptolite, in particular the interthecal septa, to compaction; all × 16. A, LO 6016t, a stipe broken 9 mm from the sicula. Cross-section shows ventrally bent interthecal septum in the mid-portion of the theca. The stippled outline indicates the compressed aperture of the previous theca. Note the difference in position of the interthecal suture on the two sides of the stipe, indicating some rotation. B, LO 6017t, a specimen broken fairly proximally (sicula not seen). The interthecal septum is disrupted and the stipe is markedly skewed. C, LO 6018t, a stipe broken 13 mm from the sicula. The proximally cut interthecal septum is intact, whereas the septum cut at mid-length is ventrally flexed.

To test our ideas we looked for suitably preserved graptolites, i.e. pyritized specimens in 'full relief', with periderm and embedded in shale. No *Clonograptus* specimen was well enough preserved for this purpose. Instead we examined a slab of black shale, from the Scanian Krapperup core, that contained several broken specimens of *Didymograptus* cf. *bifidus* from the *Phyllograptus densus* zone. All specimens had two features in common (text-fig. 1): (1), the middle part of the interthecal septum was ventrally bent, matching the observation of Rickards and Palmer (1977); and (2), the stipes were slightly skewed internally. Specimens in perfect profile view have the interthecal septum parallel to the compactional force, giving maximum resistance to compression. The observed rotation could have occurred when the interthecal septum yielded to the stress. The ventralward bending of the septum probably had to do with the compression pattern of the free distal part of the theca. This was the part that first gave way to the stress and, with a rounded ventral wall, it was natural for the ventral curvature to be accentuated. Once this bending began, it was equally natural for the tendency to progress gradually towards the proximal part of the theca.

As to the effects of flattening in our clonograptids, what can be said with certainty when comparing flattened and full relief specimens is that length measurements and thecal spacing remain the same, whereas width measurements and angles may be changed. In particular, the distal parts of simple thecae were easily affected by compression, even in pyritized specimens. The result of this compressionally induced ventral expansion would have been to increase stipe and thecal width, and also distal thecal inclination, which might change the shape of a theca from straight to somewhat curved.

It is also likely that how the specimen came to rest on the sea bottom (*via* turbiditic *vs.* quiet water descent) and the presence or absence of a period as nekroplankton would have influenced the final preservation of the rhabdosome. In comparing, for example, the types of the two closely related species *C. rigidus* (which is mostly preserved 'thecae down') and *C. milesi* (which shows most stipes in profile view), the latter seems to have had far more flexible thecae, since all were bent in the same direction (text-fig. 14) – obviously directly related to descent through the water column. This does not necessarily mean that the thecae of *C. rigidus* were more rigid; perhaps the rhabdosome spent some time as nekroplankton, partly decaying and becoming brittle, before falling to the sea bottom. To our knowledge no studies have been made of this problem.

Deformation of a rhabdosome could have been caused by other factors operating far later than the time of deposition. The effects of tectonic deformation have been studied by, for example, Cooper (1970), Jaeger (1976), and Jenkins (1980). No deformation due to regional metamorphism occurs in the Hunneberg graptolites, but some deformation is present in the types of *C. milesi*.

In the case of the Hunneberg localities, the effects of contact metamorphism must also be accounted for. All of Hunneberg is capped by a dolerite sill, in places 60 m or more in thickness. At both Mossebo and Diabasbrottet the dolerite contact lies only a few metres above the *Clonograptus*-bearing beds, and at Diabasbrottet there is another 0·5 m thick sill a few metres below them. The Mossebo section is considerably more heat-affected. In the baked layers all flattened specimens have disappeared, or survive only as faint shadows of a slightly darker colour; it is generally impossible to make any thecal measurements on such specimens. The pyritized specimens are preserved, at least as moulds, but distal parts of thecae are often missing or hard to detect, since these parts are mostly imperfectly pyritized. A specimen seen in profile view can thus appear to be thinner and have less thecal overlap than is actually the case. On the other hand, a specimen seen in dorso-ventral view (like most of the clonograptids) will show its true width.

The case against employing statistical analysis

As is evident from the above, many factors were able to deform a complicated rhabdosome like that of a clonograptid. We have not employed statistical methods, such as multivariate analysis, on our material (even though the numbers of specimens available in some cases is adequate, e.g. 150 specimens of *C. multiplex*) because:

(1) Due to the shape of the rhabdosomes, the phylogenetically important features (like details of proximal development) are visible only in very few specimens. Even the thecae are rarely seen in profile view, since this would require twisted stipes (when the measurement of inter-stipe angle will not be correct ...).

(2) Where thecae are visible, their shape may be dependent upon preservation and tectonic deformation, etc. The type of preservation also influences measurements of all types of angles.

(3) Some very important characters are based on presence/absence characters rather than measurement. Such characters can be highly dependent on preservation, e.g. bithecae.

(4) The most readily observed character, namely the length of stipes of different orders, is highly overlapping between different *Clonograptus* species (including those described herein). Specimens with cortical thickening occur in several species together with specimens without it.

This is not to say that multivariate analysis or other types of statistical treatment are always inappropriate or misleading when applied to graptolites; indeed, several studies (e.g. Cooper and Ni 1986) have produced excellent results. Generally, though, the results will be better for specimens having one or two stipes which always show the same aspect, rather than larger, multi-stiped colonies. Also, a similarity in relief between the specimens is important, not least for taxa with simple thecae.

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens. Abbreviations used are as follows: AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum (Natural History), London, Great Britain; GSC, Geological Survey of Canada, Ottawa, Canada; GSM, British Geological Survey, Nottingham, Great Britain; LO and

LR, Department of Historical Geology and Palaeontology, Lund, Sweden; PMO, Palaeontological Museum, Oslo, Norway; RM, National Museum of Natural History, Stockholm, Sweden; SGU, Geological Survey of Sweden, Uppsala, Sweden; SM, Sedgwick Museum, Cambridge, Great Britain; USNM, United States National Museum, Washington, USA.

Order GRAPTOLOIDEA Lapworth, 1875

Diagnosis (as emended by Fortey and Cooper 1986). Graptolites in which the nema is retained in the adult stage.

Discussion. Fortey and Cooper (1986) extended the Graptoloidea to include all nematophorous (i.e. planktic) graptolites, regardless of possession of bithecae, with the aim of defining a monophyletic order. Their diagnosis is based on the assumption that the planktic state was reached only once, whereas bithecae may have been lost independently in different lineages.

Suborder DICHOGRAPTINA Lapworth, 1873

Diagnosis (as emended by Fortey and Cooper 1986, and herein). Graptoloids lacking bithecae along the stipes, and without a virgella.

Discussion. Dichograptina includes all non-virgellate graptoloids except the Anisograptidae. The present emendation, '...bithecae *along the stipes...*', serves to refine this distinction, since the transition from an anisograptid structure with bithecae at all possible positions to a fully dichograptinid structure without trace of triad budding was a gradual one. We allow in Dichograptina the presence of a sicular bitheca and/or stipes showing incomplete triad budding, i.e. having the triad budding mechanism but lacking bithecae (see Pl. 83, fig. 7).

Taxa in our own collections (Lindholm 1984) indicate that this transformation took place independently along different lineages, implying that however the boundary with the Anisograptidae is defined, Dichograptina will not be a monophyletic taxon. Our emendation serves two purposes: first, to accommodate *C.* aff. *multiplex* along with *C. multiplex*, since these obviously form part of a lineage; and the second purpose is purely practical in nature, since excellently preserved material is needed to see the details mentioned.

Family DICHOGRAPTIDAE Lapworth, 1873

Diagnosis (slightly emended from Fortey and Cooper 1986). Dichograptinids lacking isograptid symmetry, number of orders of dichotomy in rhabdosome not limited; lacking prothecal folds and sigmagraptine proximal end.

Discussion. The above diagnosis includes Fortey and Cooper's (1986) diagnoses of superfamily and family, which both have to be fulfilled. They stated that the number of orders of dichtomy is limited but we have found this not to be true for clonograptids.

Many taxa included in this family are imperfectly known and their phylogenetic relationships are still tentative. Bulman (1955, 1970) divided the Dichograptidae into several 'sections' and noted (1970, p. V104) that 'No satisfactory subdivision...on a formal subfamilial basis is yet possible and the arbitrary grouping into multiramous and pauciramous genera, further tentatively divided into arbitrary "sections", is here retained'.

An attempt at a formal subdivision was made by Cooper and Fortey (1982), dividing the family into Dichograptinae, Sigmagraptinae, and Isograptinae. The latter two were raised to family rank by Fortey and Cooper (1986), whereas Dichograptinae *sensu* 1982 was divided into Dichograptinae and Tetragraptinae, provisionally excluding the pendent tetragraptids. Williams and Stevens (1988) enlarged again the Dichograptinae to include the Tetragraptinae, the pendent tetragraptids, *Xiphograptus*, and *Pseudotrigonograptus*. Dichograptinae *sensu* Fortey and Cooper (1986) includes most multiramous dichograptids and the horizontal tetragraptids.

Form genus CLONOGRAPTUS Nicholson, 1873
[= *Clonograptus* s.l.]

Type species. Graptolithus rigidus J. Hall, 1858, subsequently designated by Miller (1889).

Diagnosis (emended from Bulman 1970). Dichograptid with bilateral rhabdosome produced by dichotomous division occurring at irregular intervals; second dichotomy in most species consecutive, forming a tetragraptid proximal part, but can be delayed a few thecae; branches diverging proximally-distally diverging, subparallel, or flexuous; thecal shape variable, unknown in many species assigned to the genus; central disc unknown, secondary development of cortical overgrowth in many species, particularly in proximal parts.

Discussion. Bulman (1950) tentatively included *Clonograptus* in his new family Anisograptidae because bithecae had been found in *C. tenellus* by Stubblefield (1929); he noted (1950, p. 68) 'possibly *Clonograptus* should be divided, one genus to be included in the Anisograptidae while the other (*Clonograptus* proper) remains in the Dichograptidae'. He decided against it, since the ancestors of the latter group were certain to have had bithecae. *Clonograptus* was thus referred to the Anisograptidae in the *Treatise* (Bulman 1955, 1970). *Clonograptus* has since then been considerably depleted. The *C. tenellus* group, as defined by Lin (1981), has recently been removed from the genus, to be included within the anisograptid *Adelograptus* (Maletz and Erdtmann 1987). Another group has been removed on phylogenetic grounds and is referred to the new kinnegraptid genus *Paradelograptus* (Erdtmann *et al.* 1987). *Paradelograptus* also includes some Australian species with distinctly denticulate thecae.

Clonograptus is, for practical reasons, kept as a form genus with a phylogenetically based nominate subgenus and additional poorly known species of uncertain phylogenetic relationships. The genus is referred to the Dichograptidae, since there are no bithecae along the stipes in the type species. Any *Clonograptus* species that (on redescription) is proved to have bithecae along the stipes will have to be removed from the genus and referred to an anisograptid genus.

Two additional subgenera, *Neoclonograptus* and *Paraclonograptus* were suggested by Zhao and Zhang (1985), based on Tremadoc material from northern China. The former taxon has bithecae, and thus is not a *Clonograptus*; the latter was not described, but was still referred to as 'subgen. nov.'.

We have not attempted a complete revision of *Clonograptus s.l.*, and in this paper we only discuss species likely to belong to *Clonograptus s.s.* It could be assumed that taxa included in *Clonograptus s.l.* were derived from biradiate anisograptids along different lineages, but their ancestral Tremadoc faunas are poorly known. Maletz's collections of Scandinavian graptolites from the Upper Tremadoc *Ceratopyge* Shale show a differentiation of thecal morphology prior to the first radiation of non-bithecate graptoloids.

Subgenus CLONOGRAPTUS (CLONOGRAPTUS) Nicholson, 1873
[= *Clonograptus* s.s.; *Temnograptus* Nicholson, 1876; *Anthograptus* Törnquist, 1904; *Herrmannograptus* Monsen, 1937; ?*Calamograptus* Clark, 1924]

Type species. As for genus.

Diagnosis. Dichograptid with bilateral rhabdosome produced by dichotomous division occurring at irregular intervals; second dichotomy in most species consecutive, forming a tetragraptid proximal part, but can be delayed a few thecae; branches diverging proximally-distally diverging, subparallel, or flexuous; thecae straight or slightly curved simple tubes, overlapping one-third to two-thirds of their length; proximal development isograptid, dextral; central disc unknown, secondary development of cortical overgrowth in many species, particularly in proximal parts.

Discussion. Clonograptus s.s. is here synonymized with *Temnograptus*, *Herrmannograptus*, *Anthograptus*, and, with some doubt, *Calamograptus*. The first three of these synonymies are further discussed below, under *C. multiplex*; the possible synonymy of *Calamograptus* is discussed below under 'other species'.

Holograptus Holm, 1881, *Schizograptus* Nicholson, 1876, and *Trochograptus* Holm, 1881, are additional multiramous dichograptid genera that possess a tetragraptid proximal part and more or less irregular branching which, however, is wholly or partly lateral. Cooper and Fortey (1983) concluded that the same mechanism operated in both dichotomous and lateral stipe division. A close phylogenetic relationship could thus be suspected to exist between these genera and *Clonograptus*, but we refrain from drawing any conclusions, especially since *Schizograptus* and *Trochograptus*, which are evidently synonyms (Spjeldnaes 1986), were adapted for a rotating mode of life, in contrast to *Clonograptus*.

We include in *Clonograptus s.s.* several species with similar thecal morphology and rhabdosome development. Species included, with varying degrees of certainty, are those described or mentioned under 'other species' below. We have not been able to trace the ancestors of *Clonograptus s.s.*

Clonograptus (*Clonograptus*) *rigidus* (J. Hall, 1858)

Text-figs. 2c–e, 3, 4g–j, 5a

v 1858	*Graptolithus rigidus* n. sp. J. Hall, pp. 121–122.	
v 1865	*Graptolithus rigidus* J. Hall; J. Hall, pp. 105–106, pl. 11, figs. 1–5.	
non 1899	*Clonograptus rigidus* (J. Hall); T. S. Hall, p. 170, pl. 18, fig. 22; pl. 19, fig. 21.	
? 1935	*Clonograptus rigidus* (J. Hall); Benson and Keble, p. 271, pl. 32, fig. 2.	
v *non* 1937	*Clonograptus* cf. *rigidus* (J. Hall); Monsen, pp. 194–195, pl. 14, fig. 2.	
? 1947	*Clonograptus rigidus* (J. Hall); Ruedemann, pp. 281–282, pl. 44, figs. 10, 11.	
? 1960	*Clonograptus rigidus* (J. Hall); Berry, p. 48, pl. 5, fig. 10.	
1963	*Clonograptus* n. sp.; Ross and Berry, p. 64, pl. 2, fig. 2.	
non 1971	*Clonograptus rigidus* (J. Hall); Quilty, p. 185, text-fig. 4:4–5.	
? 1976	*Clonograptus rigidus* (J. Hall); Aceñolaza *et al.*, p. 279, pl. 1, fig. 3.	

Type material. GSC 935a–d, four slabs of partly turbiditic, rather coarse, dark grey shale containing, in addition to the illustrated types, thirteen specimens of different sizes with proximal part preserved. The descriptions and illustrations of James Hall were of rather atypical specimens (see below), but, since the lectotype has to be chosen from the originally illustrated material, we choose GSC 935b (J. Hall 1865, pl. 11, fig. 1) (text-fig. 2d herein). We have chosen this specimen instead of the larger specimen illustrated as text-fig. 2c because most specimens attain neither its dimensions nor a similar amount of cortical overgrowth.

Other material. Six specimens with preserved proximal part from the south-west end of Orleans Island, Quebec (USNM 23799); forty-seven specimens with preserved proximal part and two to five orders of stipes, found by Maletz in dark grey, often bioturbated, silty shales at loc. N of Clark (1924), Lévis, Quebec; the illustrated specimens are GSC 94896–94908 (the others have not yet received numbers but will be deposited at the GSC). The species was also found by Maletz at loc. G, Lévis, where it ranges slightly lower than *C. flexilis*. The ranges of both species do not overlap. *C. flexilis* was not found at loc. N, where the higher parts of the section are covered.

Horizon. The level of J. Hall's types and the USNM material is unknown, but the type slab (GSC 935b) is associated with one of the types of *Dictyonema murrayi* (J. Hall 1865, pl. 20, fig. 7). The newly collected topotype material from loc. N of Clark (1924) comes from 2·48–5·78 m above the 'rusty conglomerate'. The specimens are associated with *Araneograptus? murrayi*, a narrow-meshed *Dictyonema* (probably rooted), *T. approximatus* group, *T.* sp. aff. *T. decipiens*, and '*T. quadribrachiatus*', and a so far unidentified branching species, found only as stipe fragments about 1·5–2·0 mm wide, with no bithecae but with possible remnants of a triad budding mechanism. *T. approximatus* group specimens occur with the lowermost finds of *C. rigidus*.

Diagnosis. A narrow-stiped clonograptid with several orders of stipes, most specimens having somewhat prolonged first-order stipes and mostly stipes of 'rigid' appearance and approximately
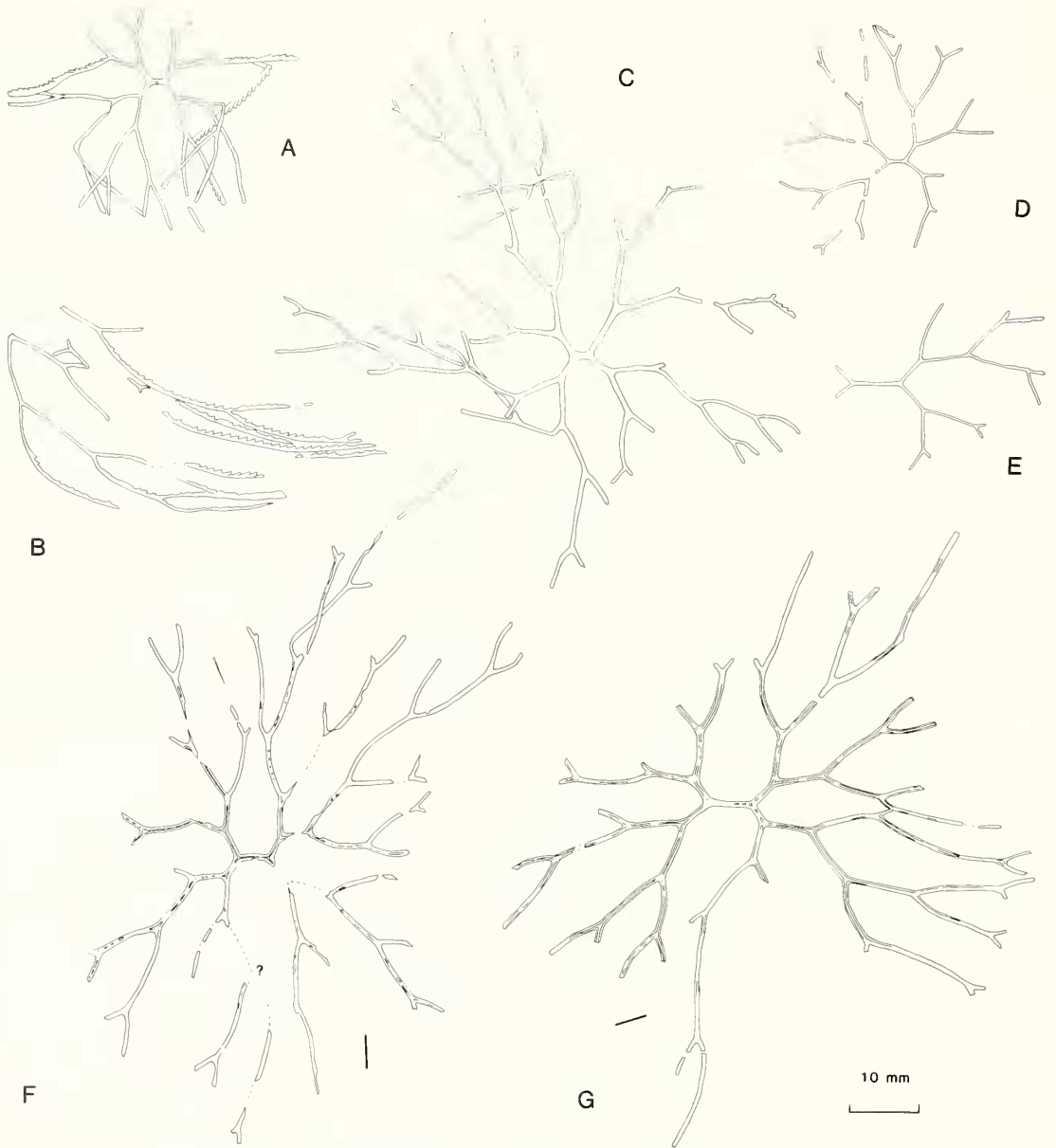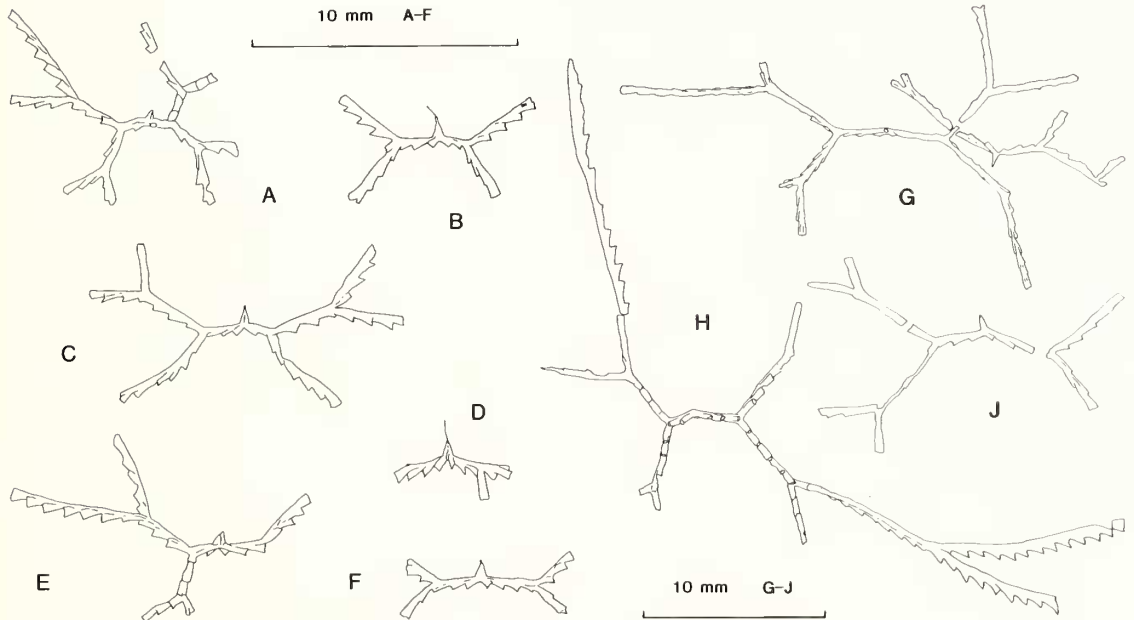
TEXT-FIG. 2. A, *Clonograptus* (*Clonograptus*) *flexilis* (J. Hall, 1858), GSC 965c, the lectotype, from Lévis, Quebec. B–G, *Clonograptus* (*Clonograptus*) *rigidus* (J. Hall, 1858). B–D, GSC 935a, c, and b, from Lévis, Quebec; specimens illustrated by J. Hall (1865), with D being the lectotype. E, GSC 935b, specimen with long first-order stipes, associated with the lectotype. F, G, USNM 23799, from Orleans Island, Quebec; compare lengths of first-order stipes with C.
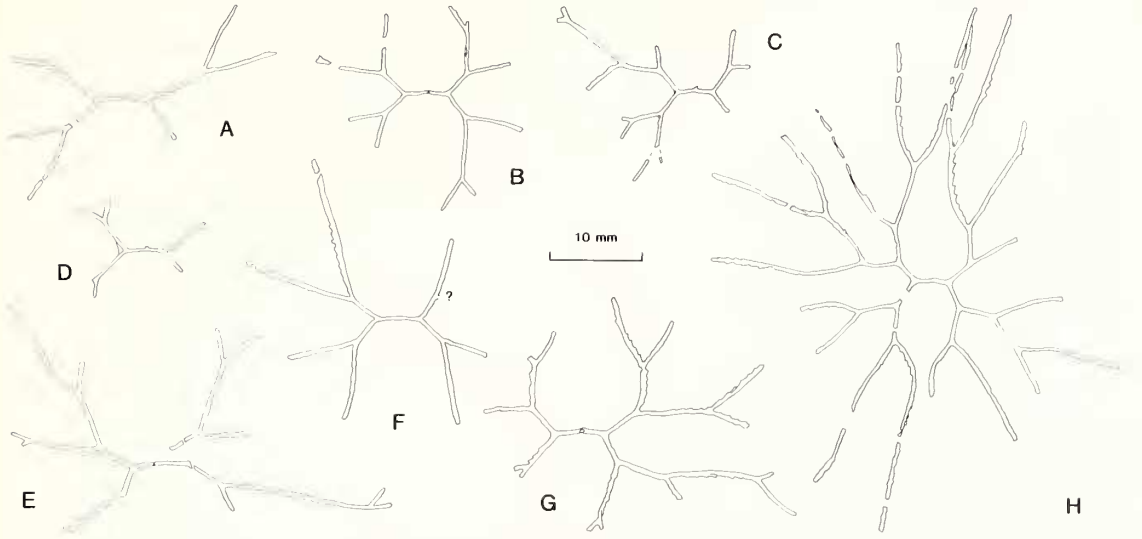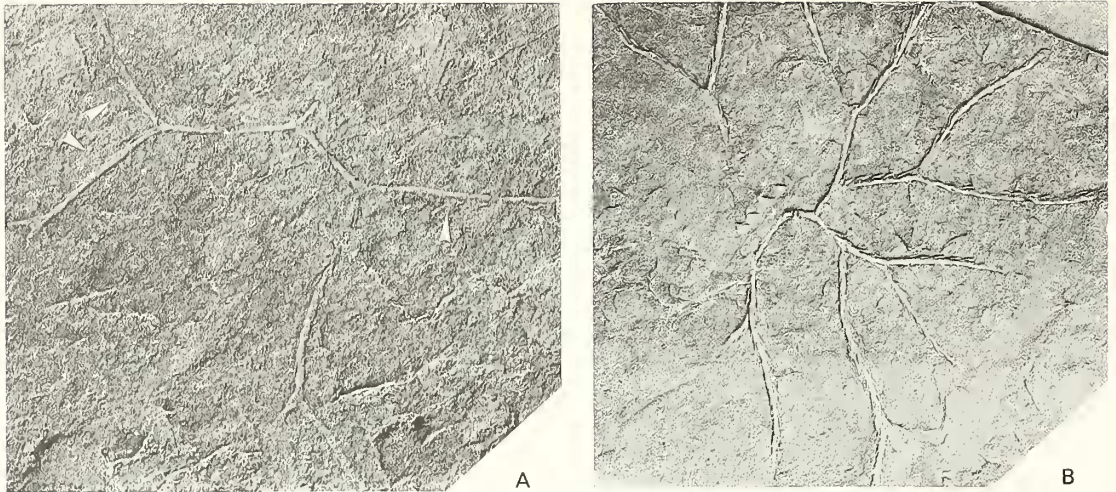
TEXT-FIG. 3. *Clonograptus* (*Clonograptus*) *rigidus* (J. Hall, 1858). A–H, GSC 94896–94903, from loc. N of Clark (1924), Lévis, Quebec, 5·58–5·66 m above the 'rusty conglomerate'; collected by J. Maletz. All specimens were found on the same surface.

TEXT-FIG. 4. A–F, *Clonograptus* (*Clonograptus*) *milesi*. AMNH 433/1-7, -3, -5 -11, -9, -12, six immature specimens associated with the types, from Monkton, Vermont. D shows a sicular bitheca and E suggests isograptid proximal development. A and F show the variation in first-order stipe length. G–J, *Clonograptus* (*Clonograptus*) *rigidus* (J. Hall, 1858), from loc. N of Clark (1924), Lévis, Quebec. G, GSC 94904, 94905, from 5·58–5·66 m above the top of the 'rusty conglomerate'. GSC 94905 has a strongly asymmetrical proximal part.
Combination of counterparts. H, GSC 94906, from a loose slab. J, GSC 94907, from same level as G.

TEXT-FIG. 5. A, *Clonograptus* (*Clonograptus*) *rigidus* (J. Hall, 1858), GSC 94908, loose slab from loc. N of Clark (1924), Lévis, Quebec; collected by J. Maletz. Latex cast of a specimen partly preserved as a high relief mould. The arrows point at the parts of the specimen with thecae in profile view, showing the lack of bithecae, × 3·5. B, *Clonograptus* (*Clonograptus*) sp. aff. *C.* (*C.*) *flexilis* (J. Hall, 1858), LO 6024t, from 'Mossebo', north-west Hunneberg, Sweden. Latex cast, × 2.

equal thickness throughout the rhabdosome. Thecae are seldom visible, but number 8·5–13 in 10 mm. There are no bithecae along the stipes. Cortical thickening occurs in some specimens.

Description. The sicula is 1·1–1·4 mm long (text-fig. 4G–J), but no specimen preserves details of proximal development. One juvenile specimen, associated with several specimens of *C. rigidus* and likely to belong to this species, shows a possible sicular bitheca. The thecae are straight tubes, sometimes bearing a short ventralward extension at the aperture, with the apertures approximately at right angles to the dorsal margin of the rhabdosome, if seen in full profile view. The thecae have a rather low inclination, about 15° in relief specimens and up to 25° when completely flattened. Thecal length is 1·3–1·7 mm, thecal width *c.* 0·2 mm, and overlap one half or less. The number of thecae in 10 mm is quite variable. The only one of Hall's illustrated specimens (text-fig. 2B) that shows a profile view (8·5–9 thecae in 10 mm) is unfortunately only a distal stipe fragment, and is thus subject to some doubt. However, it is associated with at least three other *C. rigidus* specimens with proximal part, one of which shows a few thecae of the same kind. The newly collected material has 10–13 thecae in 10 mm, but these specimens are of smaller dimensions than Hall's type, indicating a possible reduction in thecal density distalwards. There are no bithecae along the stipes (text-fig. 5A).

Stipe width in profile varies from 0·45 to 0·55 mm in relief specimens to 0·7–0·9 mm when flattened; the lateral stipe width is 0·3–0·45 mm in specimens without noticeable cortical thickening, and up to just over 1 mm in mature (gerontic?) specimens with considerable cortical thickening (text-fig. 2C, F, G).

First-order stipes usually consist of two or three thecae. Of the seventeen specimens with proximal part present on J. Hall's type slabs, six have a tetragraptid proximal end, three apparently have two thecae per first-order stipe, while eight have longer first-order stipes with a combined length of up to 7 mm. This maximum length coincides with that of the other two collections, but neither of these includes any specimens with a tetragraptid proximal part. Among the forty-seven newly collected specimens the combined first-order stipe length was 3–7 mm, distributed as follows: 1+2 thecae (three specimens), 2+2 (six), 2+3 (sixteen), 3+3 or more (seventeen); two specimens were highly asymmetrical with 2+5 and 2+6 thecae respectively; and finally three specimens were incomplete on one side, having 3, 3, and 4 thecae on the other, respectively.

Second-order stipes are *c.* 3·5–4·5 mm long (total range 2·0–8·5 mm); third-order stipes are normally 4–8 mm long (total range 3–17·5 mm). Specimens with up to eight orders of stipes are known (text-fig. 2C).

Discussion. *C. rigidus* is the type species of *Clonograptus* and was described contemporaneously with *C. flexilis* by J. Hall (1858). Since then there has been much debate on the possible conspecificity

of the two species. For example, Ruedemann (1947) and Braithwaite (1976) more or less explicitly considered *C. rigidus* a gerontic form of *C. flexilis*. Williams *et al.* (1987, p. 462) suggested 'that *C. flexilis* and *C. rigidus* may be synonymous, representing forms with little and heavy cortical thickening, respectively'. We have found no difference in this respect between the two species – some large specimens have a thick cortical cover, others do not. Characteristics separating the two species are on the average longer first- to third-order stipes, narrower stipes, more densely spaced thecae, and a shorter sicula in *C. rigidus* as compared to *C. flexilis*. Quite often the lower-order stipes of *C. rigidus* are comparatively straight, even when there is no visible cortical thickening. A large proportion of the *C. rigidus* specimens associated with Hall's illustrated types have prolonged first-order stipes, but Hall (1865) only illustrated specimens with short first-order stipes and made no mention of those with prolonged first-order stipes, nor did he assign these to another species. It has become customary to associate the name *Clonograptus* with a rhabdosome possessing a tetragraptid proximal end, yet there is some variation within and between different *Clonograptus* species: *C. rigidus* and *C. milesi* have a tendency towards prolongation, whereas *C. flexilis* and *C. multiplex* only rarely depart from the tetragraptid rule. Still, the capacity for variation seems to unite the group, and we see no reason to separate these clonograptids into different subgenera, based on first-order stipe length.

Due to the poor preservation of the type material there has been much uncertainty as to the true nature of this species, and we have failed to find any unquestionable, subsequently published identifications. In North America, *C. rigidus* has been mentioned from Newfoundland by a number of authors, but no descriptions appear to exist. The description by Ruedemann (1947) was based on topotype material but a thecal density as low as 7–8 in 10 mm is mentioned. *C rigidus* figured by Berry (1960) cannot be confirmed, due to the lack of details seen in the figure. *Clonograptus* n. sp. figured by Ross and Berry (1963, pl. 2, fig. 2) might be conspecific with *C. rigidus* since it has prolonged first-order stipes, and the shape and thecal characteristics are not incompatible with this species.

Of the Australian reports, the *C. rigidus* of T. S. Hall (1899) was probably misidentified, since the thecae are said to be curved. *C. rigidus* of Quilty (1971) is obviously an older, presumably anisograptid form. The species was also mentioned from New Zealand by Benson and Keble (1935); they gave no description, but their illustrated specimen shows one primary stipe of two thecae. The branching density is very similar to that of *C. rigidus*, but the stipes appear to be thinner and the thecal characteristics cannot be seen.

C. rigidus has also been reported from South America (Aceñolaza *et al.* 1976), but the thecal density of the illustrated specimen appears to be too low (there is some doubt, however, about the magnification of the photo).

Monsen's (1937) *C.* cf. *rigidus* from Norway is a form with much cortex, showing thecae on a distal stipe. These have very little overlap and expand towards the aperture ('*tenellus* type').

C. rigidus was also reported by Bjerreskov and Poulsen (1973) from northern Greenland. An examination of the material has shown it to be another species, not corresponding to any named species we know of. Its dimensions are slightly smaller than those of *C. rigidus*. The most mature specimen has a considerable overgrowth of cortex. Bithecae were not seen, so it is possible that the species belongs to *Clonograptus s.s.* Its age is within the Lancefieldian La2–La3 range. The fauna is presently being studied by Merete Bjerreskov.

Clonograptus (*Clonograptus*) *flexilis* (J. Hall, 1858)

Text-figs. 2A, 6A–E

v 1858   *Graptolithus flexilis* n. sp. J. Hall, pp. 119–120.
v 1865   *Graptolithus flexilis* J. Hall; J. Hall, pp. 103–104, pl. 10, figs. 3–9.
  1895   *Clonograptus flexilis* (J. Hall); Pritchard, pp. 29–30.
? 1899   *Clonograptus flexilis* (J. Hall); T. S. Hall, pp. 169–170, pl. 19, fig. 20.

v *non* 1937 *Clonograptus* cf. *flexilis* (J. Hall); Monsen, pp. 195–196, pl. 6, figs. 1, 3, 8.
       1947 *Clonograptus flexilis* (J. Hall); Ruedemann, pp. 280–281, pl. 44, figs. 4–9.
non 1960 *Clonograptus flexilis* (J. Hall); Berry, p. 47, pl. 6, fig. 4.
   ? 1963 *Clonograptus flexilis* (J. Hall); Ross and Berry, pp. 72–73, pl. 1, figs. 5, 7; pl. 2, fig. 1.
       1967 *Clonograptus flexilis* (J. Hall); Cumming, fig. 2.
non 1976 *Clonograptus flexilis* (J. Hall); Braithwaite, pp. 15–19, pl. 3, figs. 1, 4–8. [Topotype specimens seen.]
   ? 1979 *Clonograptus flexilis* (J. Hall); Wang *et al.*, pp. 501–502, pl. 1, fig. 11; text-fig. 10 B.
   ? 1983 *Clonograptus flexilis taipingensis* n. ssp. Li, p. 146, pl. 1, fig. 1.
       1987 *Clonograptus flexilis* (J. Hall); Williams *et al.*, fig. 5 D–H.

Type material. GSC 965a-d, four slabs of dark shale from Lévis, Quebec. There are only a few specimens on these slabs in addition to the six illustrated by Hall (1865). A holotype was not selected by James Hall, nor has there been any subsequent designation of a lectotype. We therefore choose as lectotype a specimen on slab GSC 965c (J. Hall 1865, pl. 10, fig. 5) (text-fig. 2 A herein). A 'holotype' for *C. flexilis* was erroneously selected by Braithwaite (1976) from this Utah material.

Other material. Twenty-eight topotype specimens, LO 6019t–6023t and LR 1–23, ranging from four-stiped to mature. These specimens are preserved in dark shale and are flattened or in low relief. All are from Lévis, USGS loc. 219, which is identical to the railroad cut described by Raymond (1914) and to loc. G of Clark (1924). Additional information on the locality was given by Landing and Benus (1985). All specimens come from the lower fossiliferous horizon mentioned by Raymond (1914) and are labelled *Dichograptus flexilis* (allegedly by Gurley). The material belongs to the Törnquist collection of Lund University.

Horizon. All specimens derive from a fauna 'confined apparently to a very narrow vertical range' (Raymond 1914, p. 527). Recent field work at loc. G by Maletz has established the range as 8·05 m, starting from 4·45 m above the top of the 'rusty conglomerate'. These specimens have as yet not been studied in detail and are not included in this study. The following species are associated with *C. flexilis*: *Tetragraptus approximatus* group, '*T. quadribrachiatus*', a four-stiped species with the same stipe growth-habit as *Tetragraptus phyllograptoides*, but evidently unrelated to it [= *T. phyllograptoides* cf. *phyllograptoides sensu* Williams and Stevens (1988)], *Pendeograptus fruticosus*, *Didymograptus constrictus*, *D. similis*, *Phyllograptus* sp. [= *P. ilicifolius* according to label by Gurley], and a rooted dendroid [= *Callograptus salteri* Hall according to label by Gurley]. The assemblage indicates the Arenig *T. akzharensis* zone of Williams and Stevens (1988). Williams *et al.* (1987, p. 462) reported having found the species already in the uppermost Tremadoc.

Diagnosis. A clonograptid with tetragraptid proximal part and irregular branching. Thecae straight and tubelike, 9–9·5 in 10 mm; stipe width in profile view 1·0–1·8 mm. Several orders of stipes. Highly variable cortical cover. No bithecae have been observed.

Description. Four immature flattened specimens (see text-fig. 6D, E) are preserved in profile view, showing the sicula, which is 2·0–2·4 mm long and 0·4 mm wide across the aperture. In all specimens the nema is broken off close to the prosicula. The first bud arises within 0·5 mm of the sicular apex. Due to flattening, the proximal development type cannot be identified with certainty.

The thecae are straight tubes, with their apertures approximately at right angles to the dorsal margin of the rhabdosome. They are inclined at 19–32° if seen in full profile view. The maximum variation in one specimen is *c.* 5–7°. The thecae are 2·2–3·0 mm long and *c.* 0·4–0·6 mm wide. Stipe width is 1·0–1·8 mm. There are 9–9·5 thecae in 10 mm, and thecal overlap ranges from just above one half to slightly less than two-thirds. No bithecae have been seen.

In dorsal view stipe width varies with the amount of cortex. This is especially obvious in first-order stipes, which are 0·4–1·0 mm wide (cf. text-fig. 6A–C). Second and higher orders measure 0·4–0·5 mm in specimens with little cortex and 0·5–0·6 mm (occasionally 0·7 mm) in heavily cortex-covered rhabdosomes. Characteristically the latter are the largest specimens.

First-order stipes consist of one theca. Two aberrant immature specimens (LR 1–2) were found, though, with one and both of the primary stipes respectively consisting of two thecae. The second dichotomy encloses an angle of 90–110°, and the ensuing second-order stipes consist of one, two, or three thecae. The next dichotomy encloses 55–95° (mode at 75–80°), and third-order stipes are usually 3–7 mm long, in most specimens of unequal length. More distally the concept of stipe order is hardly applicable – the variation in stipe length being

10 mm (ABCF)
2 mm (DE)

A

B

C

D

E

F
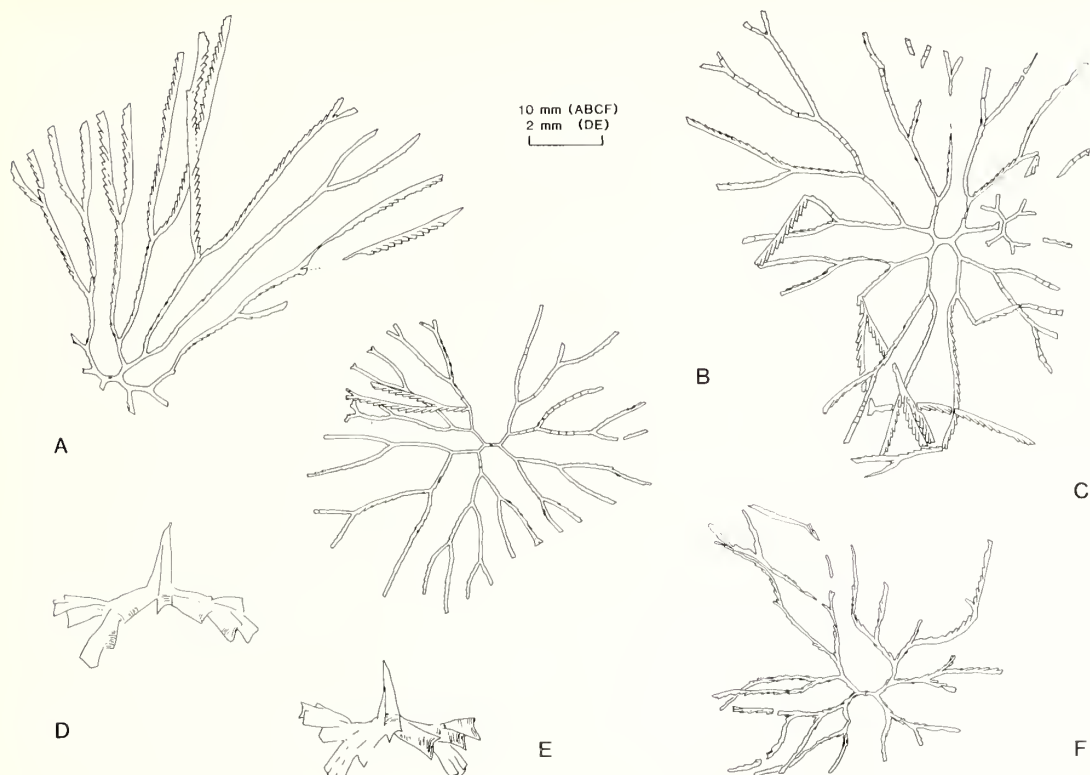
TEXT-FIG. 6. A–E, *Clonograptus* (*Clonograptus*) *flexilis* (J. Hall, 1858), from USGS loc. 219, Lévis, Quebec. A–C, three mature specimens showing the variation in stipe length, stipe width, and amount of cortex. A, LO 6019t, a specimen with much cortex and an unusually long fourth-order stipe. B, LO 6020t, one of the largest specimens without appreciable cortical thickening. The lower half of the figure shows the tendency of the graptolite to infill 'empty spaces' between stipes: the limited branching to the right is compensated for by an expansion of the left-hand lobe. C, LO 6021t, a mature specimen with cortical thickening, associated with an immature specimen with little cortex. D, E, LO 6022t and LO 6023t, two immature specimens showing the sicula. F, *Clonograptus* (*Clonograptus*) sp. aff. *C.* (*C.*) *flexilis* (J. Hall, 1858), RM Cn1467, from 'Mossebo', north-west Hunneberg, Sweden; collected by Holm.

too great. Among the measured specimens 'fourth-order stipes' range from 3·5 to 35 mm in length. The angle of dichotomy generally decreases slightly away from the proximal part, but untwisted stipe pairs never show an angle less than 45–50°.

Discussion. The possible synonymy of *C. flexilis* and *C. rigidus* has been much debated. For a discussion of this, and the differences between the two taxa, see the description of *C. rigidus* above.

C. flexilis has been reported for many areas of the world, but it has not always been correctly identified. *C. flexilis* of Berry (1960) is a very thin form and *C. flexilis* of Ross and Berry (1963) must be subject to some doubt, since the thecal parameters, as seen from their figures, do not suggest conspecificity with *C. flexilis*. The specimen illustrated by Cumming (1967) is unquestionably a *C. flexilis*, whereas those figured by Williams *et al.* (1987) are mostly fragmentary and only their fig. 5H can be positively identified. Interestingly, their fig. 5D shows prolonged first-order stipes.

An Australian Lancefieldian form was described, but not figured, as *C. flexilis* by Pritchard (1895). The description conforms to our material, except for a slightly closer thecal spacing: 10–11 as opposed to 9–9·5 thecae in 10 mm. The species was redescribed and illustrated by T. S. Hall

(1899). His illustration was drawn from one of Pritchard's specimens, but shows tapering stipes, devoid of thecae (as also mentioned in the description). However inconsistent these two descriptions may seem, there is one plausible explanation. We have seen *Clonograptus* specimens with stipes in profile view but thecae only visible on a wetted surface. On a dry slab the stipes are seen to taper, reflecting the distally diminishing cortex on the 'common canal'. Since Pritchard actually saw the relevant thecal characters, the identity of the taxon is established in his case, but this is, of course, no guarantee that every clonograptid appearing to have narrowing stipes belongs to *Clonograptus s.s.*, especially if thecal shape differs in proximal and distal parts of the rhabdosome.

Monsen's (1937) *C.* cf. *flexilis* from Scandinavia, if correctly illustrated, is a mixture of two species. Unfortunately this cannot be verified, since the specimen shown on her pl. 6, fig. 3 has been destroyed. The other specimens are herein referred to *C. galgebergi*.

The taxon has also been reported from China (Wang *et al.* 1979) but thecal details are unknown in the specimen described. A new subspecies was described by Li (1983) as *C. flexilis taipingensis*; it probably does belong to *Clonograptus s.s.*, but we cannot judge if it is conspecific with *C. flexilis*.

We conclude that the only definite occurrences of *C. flexilis* are limited to Canada and Australia.

Clonograptus (*Clonograptus*) sp. (spp. ?) aff. *C.* (*C.*) *flexilis* (J. Hall, 1858)

Text-figs 5B, 6F

Material and horizon. Only three specimens are known. Specimen 1 (with counterpart), RM Cn1467–1468 (text-fig. 6F), was found on a slab of black shale in the Riksmuseum collection, labelled 'Hunneberg, Mossebo'. It is likely to come from a level 1–1·5 m below the local *C. multiplex* beds, as evidenced by the co-occurrence of extensiform didymograptids of *D. constrictus-D. similis* type and the conodont *Oelandodus elongatus*. The indicated level is low in the range of the didymograptids and high in the range of the conodont. The specimen is preserved in part-relief: the thecae are flat, and only visible if wetted, whereas the 'common canal' is seen in relief.

Specimen 2, LO 5868t (text-fig. 5B), derives from higher up in the same section. It comes from a loose slab of slightly thermally altered black shale, and is associated with *Trichograptus dilaceratus* (Herrmann, 1885) which first appears in the higher ranges of the *C. multiplex* beds. The specimen is preserved as a high relief mould.

Specimen 3, LO 1737, from the *Didymograptus balticus* Zone of Flagabro, Scania, Sweden, was referred to as 'undetermined irregular Dichograptidae' by Törnquist (1904, pl. 2, fig. 24). It is preserved in low relief in grey shale.

Description. Specimen 1 has six orders of stipes. The second to fourth orders are 2–3·5 mm, 2–6 mm, and 4–16 mm long, respectively. Stipe width in profile reaches a maximum of 1·0 mm, and there are *c.* 10 thecae in 10 mm. Thecae are straight and inclined at 15–20°. Thecal overlap is approximately one half.

The corresponding figures for specimen 2 are: four orders of stipes; stipe lengths 3 mm, 3·5–7 mm, and up to at least 13 mm; width 0·8 mm; 9·5 thecae in 10 mm; thecal inclination 10–15°; thecal shape and overlap similar to specimen 1.


EXPLANATION OF PLATE 83

Figs. 1–6. *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868). 1, LO 6025t, immature specimen in profile view, showing the proximal development, × 9. 2, LO 6026t, specimen illustrating the mode of stipe division, × 10. 3, 4, LO 6027t, LO 6027 +, counterparts of the proximal part of a specimen showing (arrow) a possible bithcca or an aborted stipe, × 8. 5, 6, LO 6028t, LO 6028 +, counterparts of a 'trichotomy', i.e. two consecutive dichotomies, × 10. 1, from 'Mossebo', north-west Hunneberg, Sweden; collected by Westergård. 2–6, from Diabasbrottet, north-west Hunneberg, Sweden; collected by J. Maletz.

Fig. 7. *Clonograptus* (*Clonograptus*) sp. aff. *C.* (*C.*) *multiplex* (Nicholson, 1868), PMO 108.558, stipe fragment showing (arrows) a triad budding mechanism without bithecac, × 9. From Slemmestad, Norway; collected by N. Spjeldnaes.

All photographs were made from latex casts.

PLATE 83

LINDHOLM and MALETZ, *Clonograptus*
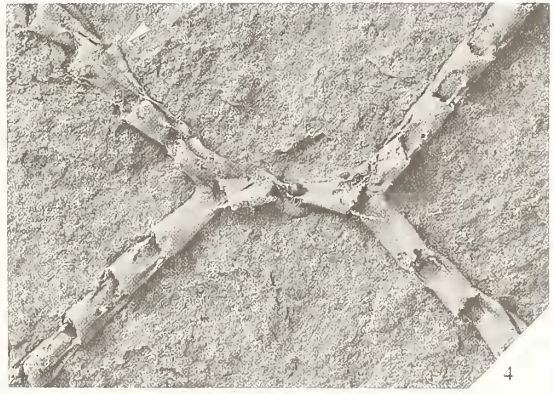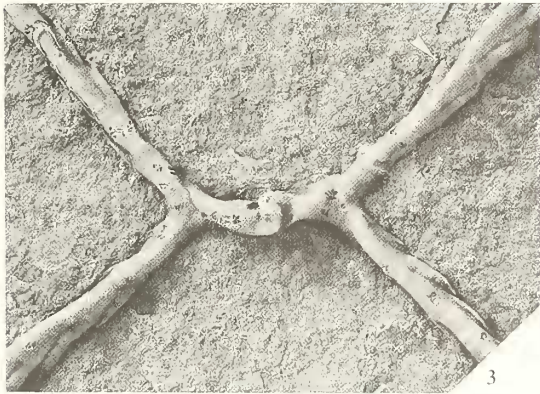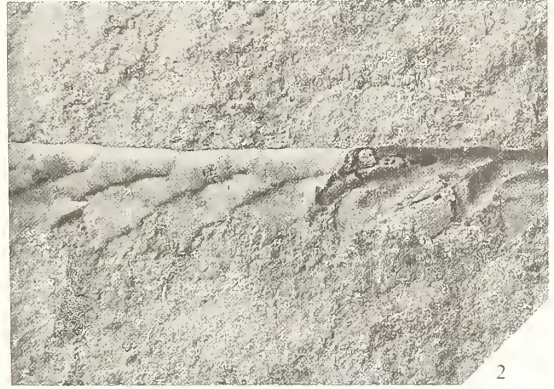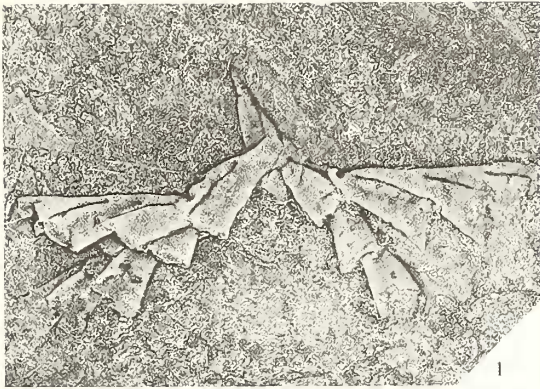
Specimen 3 is very similar to specimen 2 and they are undoubtedly conspecific.

None has any noticeable cortical thickening. Specimen 1 appears to have had more flexible stipes and slightly lower angles of divergence of stipes.

Discussion. The three specimens share many features, yet certain differences make it difficult to decide whether they are conspecific. There is also a slight difference in stratigraphic horizon. All show a similarity to *C. flexilis*, especially in overall size and branching pattern. Specimens 2 and 3 bear a certain resemblance to *C. multiplex* in stipe attitudes, but are smaller than any of our specimens of that species.

Clonograptus (*Clonograptus*) *multiplex* (Nicholson, 1868)

Plate 83, figs. 1–6; text-figs. 7–11

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v 1868	*Dichograpsus multiplex* n. sp. Nicholson, pp. 129–130, pl. 6, figs. 1–3.	
v 1876	*Temnograptus multiplex* (Nicholson); Nicholson, p. 248, pl. 9, fig. 1.	
v 1882	*Dichograptus* (?) *Milesi* (J. Hall); Herrmann, pp. 351–352, pl. 2, figs. 17, 18.	
v 1885	*Clonograptus* sp. Herrmann, p. 88, fig. 11.	
v 1886	*Clonograptus multiplex* (Nicholson); Herrmann, p. 25, fig. 9.	
v 1898	*Temnograptus multiplex* (Nicholson); Elles, p. 477, fig. 6.	
v 1902	*Temnograptus multiplex* (Nicholson); Elles and Wood, p. 86, pl. 12, fig. 1; text-fig. 48.	
v 1904	*Temnograptus multiplex* (Nicholson); Törnquist, pp. 21–22, pl. 3, figs. 1–4.	
v 1904	*Dichograptus regularis* n. sp. Törnquist, p. 20, pl. 2, fig. 19.	
v 1904	*Anthograptus nidus* n. sp. Törnquist, pp. 22–23, pl. 4, figs. 4, 5.	
vp 1904	Undetermined irregular Dichograptidae; Törnquist, p. 22, pl. 2, figs. 22–23 (*non* pl. 2, fig. 24 = *C.* sp. aff. *C. flexilis*).	
v 1937	*Herrmannograptus milesi* (J. Hall); Monsen, pp. 190–191, pl. 5, fig. 31; pl. 14, fig. 10; pl. 15, fig. 9.	
vp 1937	*Herrmannograptus regularis* (Törnquist); Monsen, p. 192, pl. 14, figs. ?3, ?8, 9 (figs. 3 and 8 are part and counterpart of an indeterminate stipe fragment).	
? 1987	*Temnograptus regularis* (Törnquist); Xiao, p. 630, pl. 2, fig. 1.	

Type material. BMNH Q31 contains the two types. We choose as lectotype the most complete specimen, shown as the uppermost specimen of Elles and Wood (1902, pl. 12, fig. 1). It and its counterpart, GSM 7648, are illustrated as text-fig. 7 herein. The other type specimen has an asymmetrical proximal end, with one first-order stipe consisting of presumably five thecae, the other of one theca only. Its counterpart is SM A.17950. The material comes from the Skiddaw Slate Group at Peel Wyke at the north-west end of Bassenthwaite lake, Lake District, England. The lithology is a dark grey, fine-grained turbiditic siltstone. The types have suffered some tectonic distortion and are badly preserved. There appear to be 8–10 thecae in 10 mm.

Other material. LO 1738t, 1748T, 6025t–6056t and available counterparts, LR 24–132, five unnumbered SGU specimens, and RM Cn1463 and Cn1828, all with proximal parts preserved, and additionally numerous stipe fragments. Specimens are of all sizes, from four-stiped to giants. The material is partly flattened and partly in relief, and derives from shale, which in parts of the succession is contact-metamorphosed by an overlying dolerite sill. The described fauna comes from two localities at north-west Hunneberg, Sweden: Mossebo and Diabasbrottet, situated approximately 1 km apart. The 'Mossebo' of authors before Tjernvik (1956) is identical to Diabasbrottet.

Horizon. Lower Arenig, lower part of the *D. balticus* Zone *sensu* Törnquist (1901).

Diagnosis. A large-sized clonograptid with highly irregular branching. The proximal part is tetragraptid; second-order stipes vary from short to very long, the variation occurring both within and between specimens. The thecae are somewhat curved tubes, mostly spaced 8·5–10 in 10 mm; stipe width is 1·2–1·7 mm. There are no bithecae.

Description. A few immature specimens preserved in profile view have been found, of which one is in full relief (Pl. 83, fig. 1). The sicula is *c.* 1·8–2·2 mm long and 0·6–0·7 mm wide across the aperture. A nema was not
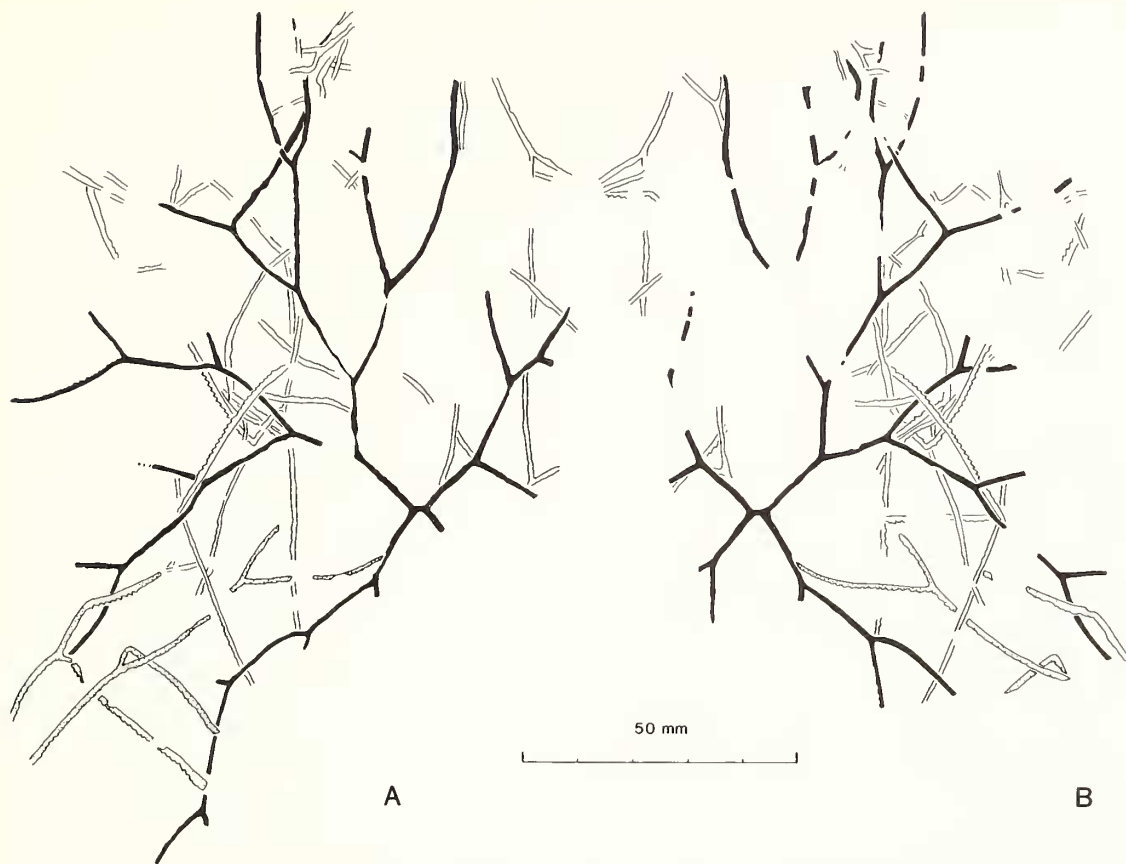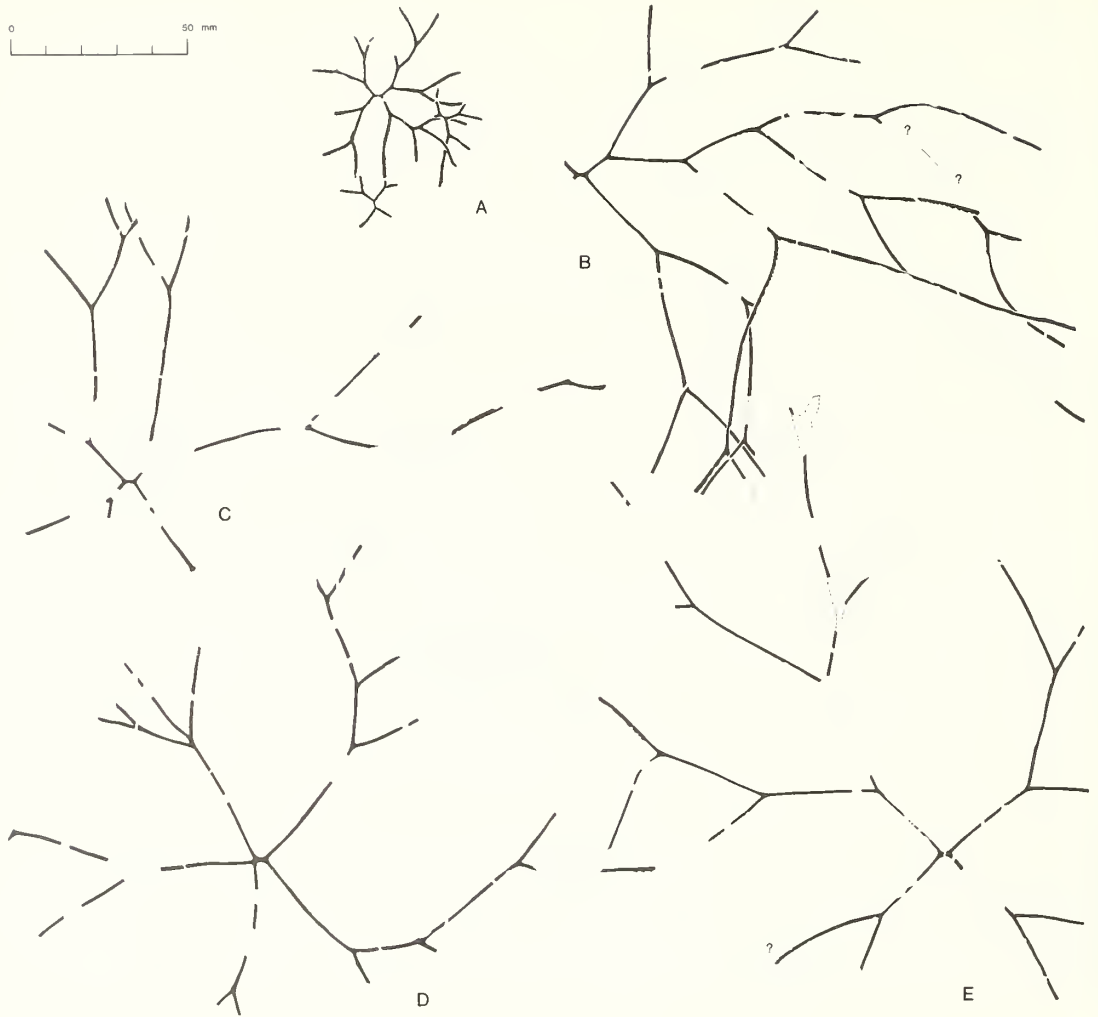
TEXT-FIG. 7. *Clonograptus (Clonograptus) multiplex* (Nicholson, 1868). A, BMNH Q31, the lectotype. The specimen was figured by Nicholson (1868, 1876) and Elles and Wood (1902). B, GSM 7648, counterpart of lectotype, showing the total length of all the second-order stipes. From Peel Wyke, Lake District, England. The specimen is shown in black; stippled parts of this specimen are seen only as faint traces. Stipes belonging to the other type are dotted, stipes not belonging to either specimen are outlined for easier comparison with the illustration by Elles and Wood (1902, pl. 12, fig. 1).

preserved in any specimen. There is no sicular bitheca. The proximal development is isograptid, dextral (defined by Cooper and Fortey 1982, p. 172). Th1^1 buds within 0·5 mm of the sicular apex. Th1^2 arises from th1^1 half way down the sicula. The next dichotomy is consecutive, resulting in first-order stipes of one theca each, whereas the following dichotomies are nearly always delayed. We have found no specimen with prolonged first-order stipes in the Hunneberg fauna. The thecae are simple tubes, slightly curved, and overlap for about half their length. The aperture is gently concave. Thecal length, and thus stipe width, varies somewhat. The inclination of thecae seen in full profile view is 15–25° proximally and 30–40° distally. Thecal spacing is variable, normally 8·5–10 thecae in 10 mm (total range 7·6–10·5). Profile stipe width is equally variable at 1·2–1·7 mm, but there is no correlation between thecal spacing and stipe width. Lateral stipe width is *c*. 0·5–1·0 mm.

The stipes are of normal dichograptid appearance, without bithecae or other signs of triad budding mechanism. There is one peculiar specimen, however, showing a structure which could be either a bitheca or an aborted stipe (Pl. 83, figs. 3, 4). Stipe length of all orders except the first is extremely variable; see text-figs. 8 and 9 representing three associations, and text-fig. 10 illustrating the range in stipe length and intra-specimen variation. Stipes are relatively straight or gently curved unless affected by water currents (text-fig. 10A). Straight stipes are most common in specimens with long second-order stipes (i.e. less crowding of stipes). The
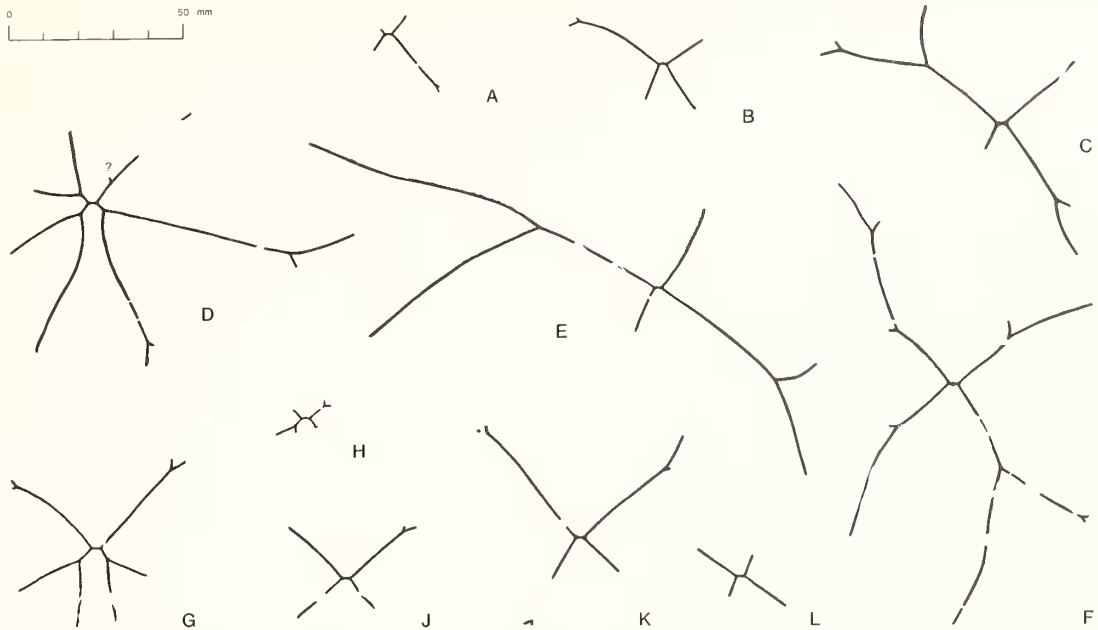
TEXT-FIG. 8. *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868). A and B–E represent two natural assocations showing the size range and irregular branching of this species. A, LO 6029t–6031t are specimens at the lower end of the size range; note 'trichotomy' in the largest specimen. From 'Mossebo'; collected by Moberg and von Schmalensee. B–E, LO 6032t–6035t and counterparts. Note the two 'trichotomies' in D. Only E has a symmetrical proximal part. Stippled parts of the specimens are seen only as a slightly darker colour of the shale; no impression or periderm is left. Dashed outlines represent pyrite concretions. Baked shale from Mossebo; collected by K. Lindholm.

size-range of second-order stipes is from 1 to more than 40 mm. Specimens with all four second-order stipes of subequal length (i.e. with the longest stipe less than twice the length of the shortest one) seem to be somewhat more common than the highly irregular ones. About half the specimens have short second-order stipes, *c.* 4–10 mm long.

The range in length of higher-order stipes is even greater. As in *C. flexilis*, it is debatable if the concept of stipe order has much meaning. Stipes are from 1 mm long (Pl. 83, figs. 5, 6; text-figs. 8D, 10C, 11A, B) in connection with 'trichotomies' and 'quadrichotomies' (i.e. two or three consecutive dichotomies; cf. *Anthograptus nidus*), to at least 75 mm. The angle of the second dichotomy is normally 90–100° (total range

TEXT-FIG. 9. *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868). A-L, LO 6036t–6046t and counterparts, eleven associated specimens showing the variation in second-order stipe length. Baked shale from Mossebo; collected by K. Lindholm.

70–120°). The mode of the third dichotomy is 60–70° (total range 50–95°), and 60° for the fourth to sixth dichotomies (total range 40–80°). Up to seven or eight stipe orders are present in the largest specimens.

To exemplify the size variation, text-fig. 8 A shows a specimen with fifth-order stipes starting 16 mm from the sicula, whereas the same point is 104 mm away in text-fig. 8 E. Text-fig. 9 E shows a specimen which retains third-order stipes 88 mm from the sicula. The specimen in text-fig. 8 E has a diameter of at least 390 mm, whereas the dimensions of text-fig. 8 A are fairly close to those of *C. flexilis*.

Discussion. Due to the extreme variability and the few specimens available to different authors, specimens of this species have been referred to diverse genera and sometimes also split into different species. It certainly requires the number of specimens we have seen to appreciate properly the intraspecific variability.

Specimens belonging to *C. multiplex* have on various occasions been referred to the genera *Dichograptus* Salter, 1863, *Temnograptus* Nicholson, 1876, *Clonograptus* Nicholson, 1873, *Herrmannograptus* Monsen, 1937, and *Anthograptus* Törnquist, 1904. Of these, *Dichograptus* was considered inappropriate for this species very early and *Herrmannograptus* was discarded by Bulman (1955) as a synonym of *Clonograptus*. Since the majority of Monsen's (1937) *Herrmannograptus* specimens belong to *C. multiplex*, the type species of *Temnograptus*, this supports the synonymy of *Clonograptus* and *Temnograptus*. The only visible difference between these 'genera' is stipe length, especially the possibility of longer second-order stipes in *Temnograptus*. However, the great variation in this respect of '*T.*' *multiplex* casts doubt upon the validity of this character for generic distinction. We therefore consider *Temnograptus* to be a synonym of *Clonograptus*.

Anthograptus (text-fig. 11 C) is more of a problem. It was originally described from one fragment without a proximal end. The only similar specimen we have found (text-fig. 11 B) likewise lacks the proximal part, so here we must rely on circumstantial evidence. First, our specimen is associated with an apparently normal *C. multiplex* specimen. We also have eight specimens of *C. multiplex* with
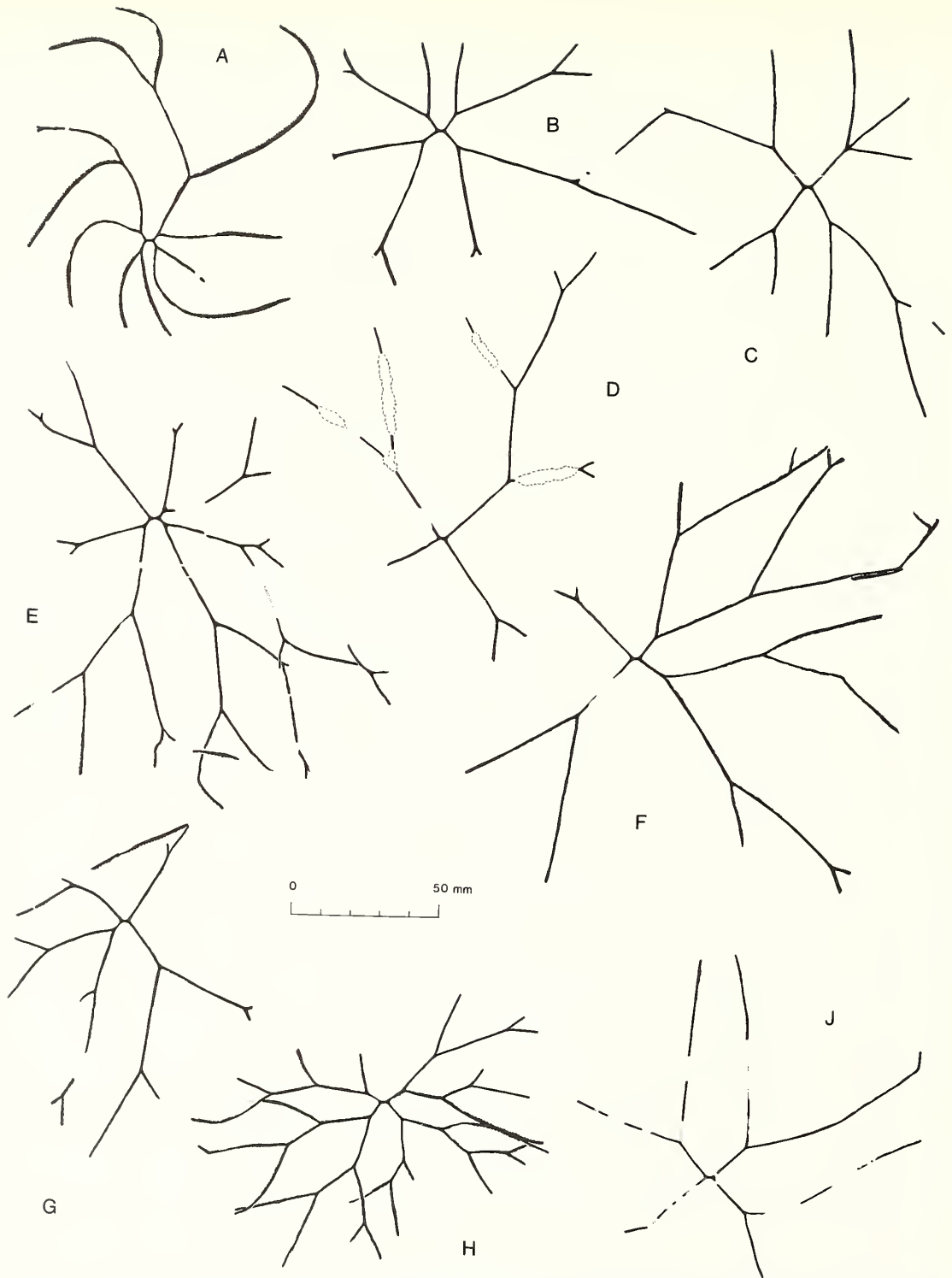
TEXT-FIG. 10. Stipe length variation in *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868). A–D, LO 6047t–6050t, have symmetrical proximal parts of varying second-order stipe length. E–G, LO 6051t–6053t, have irregular proximal parts with respectively one, two, and three long second-order stipes (cf. also text-fig. 6G). H, J, LO 6054t, 6055t, show the variability in higher-order stipe lengths. A, G, and H are combinations of both counterparts. Stippling and dashed outlines as in text-fig. 5. A, C, E, F, and H are from Diabasbrottet; collected by J. Maletz. B is from Mossebo. D and J are from Mossebo; collected by J. Maletz. G is from 'Mossebo'; collected by Moberg and von Schmalensee.
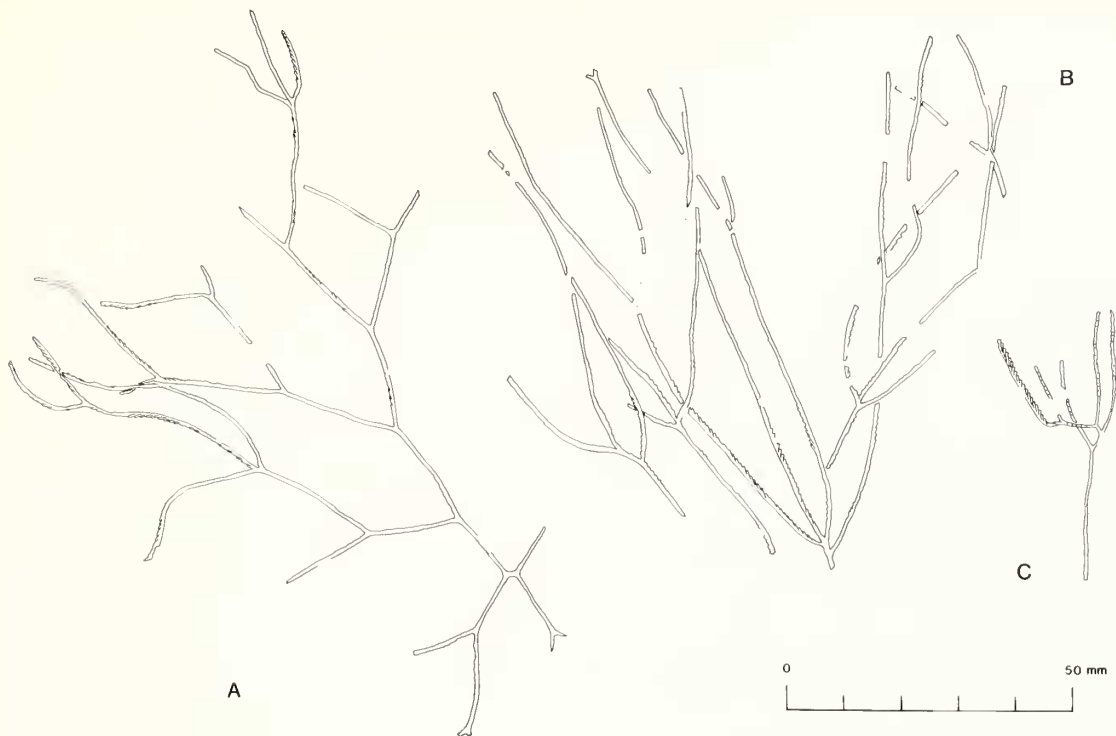
TEXT-FIG. 11. A, B are specimens of *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868) suggesting synonymy with *Anthograptus nidus* Törnquist, 1904 (c). A, LO 1738+, counterpart of Törnquist's (1904) pl. 3, fig. 1, which was reproduced as a reconstruction by Bulman (1955, 1970). Note the irregularly placed 'trichotomies', which were not figured by Törnquist. From 'Mossebo'; collected by Moberg and von Schmalensee. B, LO 6056t, stipe fragments of a very large specimen showing 'trichotomies' and a 'quadrichotomy'. Baked shale from Mossebo; collected by K. Lindholm. c, LO 1748T, holotype of *Anthograptus nidus* Törnquist, 1904, herein synonymized with *C. multiplex*. From 'Mossebo'; collected by Törnquist.

a 'trichotomy' and preserved proximal part (see, for example, text-figs. 8 and 11). The 'trichotomies' are erratic, occurring from second to seventh order. Text-fig. 11 B can be considered as an aberrant specimen that systematically employed this mode of branching. Judging from the size of the specimen, the most proximal stipes seen are of third or higher order. The mode of branching strikingly resembles that of *Orthodichograptus robbinsi* Thomas, 1973, but thecal characteristics are identical to those of *C. multiplex*. We therefore regard *Anthograptus* as a synonym of *Clonograptus*, and dispute its affiliation to the Schizograpti by Bulman (1955, 1970). A mode of branching consisting exclusively of 'trichotomies' is used by *Triaenograptus* T. S. Hall, 1914, from higher parts of the Arenig in Victoria; it was considered by Bulman (1970) to be synonymous with *Tridensigraptus* Zhao, 1964, from eastern China. These forms have geometrically arranged stipes, which is unknown in *C. multiplex*; this was possibly an adaptation to a special mode of life, rather than an indicator of phylogenetic relationship.

Törnquist's (1904) *Dichograptus regularis* is based on one specimen of *C. multiplex* with short second-order stipes and longer than average third-order stipes. The specimen thus superficially resembles a *Dichograptus*. A similar specimen, carrying stipes of higher orders, is shown in text-fig. 10B. Some of Törnquist's (1904) 'undetermined irregular Dichograptidae' also belong without any doubt to this species. Irregular specimens are not uncommon in a larger collection (cf., for example, text-figs. 9G, 10E–G).

TEXT-FIG. 12. *Clonograptus* (*Clonograptus*) sp. aff. *C.* (*C.*) *multiplex* (Nicholson, 1868). A, PMO 108.557, 108.558, from Slemmestad, Norway; collected by N. Spjeldnaes. B, SGU Type 5468, from 'Mossebo'; collected by von Schmalensee.

The name *C. multiplex* has not been used since Törnquist (1904). Monsen (1937) divided her '*Herrmannograptus*' into three species, based on increasing length of second-order stipes: *H. milesi*, *H. regularis*, and *H. galgebergi*. We consider *C. galgebergi* valid, but based on other criteria than Monsen's. The other two 'species' are included in *C. multiplex*. The use of the name *milesi* is based on a misunderstanding taken over from Herrmann (1882) (see below, under *C. milesi*).

Clonograptus sp. B of Kraft and Mergl (1979) could well be synonymous with *C. multiplex*. It is badly preserved, in a rather coarse sediment (which may explain its apparently narrower stipes; cf. 'Preservation' p. 714). It has a thecal spacing of 11–12 in 10 mm, slightly more crowded than our material, but it exhibits the same irregularity of the proximal part.

Clonograptus (*Clonograptus*) sp. aff. *C.* (*C.*) *multiplex* (Nicholson, 1868)

Plate 83, fig. 7; text-fig. 12

Material. One specimen, PMO 108.557–108.558, from 'Roykenveien, S. Slemmestadskryssct (N-siden av veien)' ('Røyken Road, south of Slemmestad cross-roads (north side of the road)'), Slemmestad, Oslo region, Norway (text-fig. 12A). One specimen, SGU Type 5468, from 'Mossebo Limestone Quarry', north-west Hunneberg, Sweden (text-fig. 12B).

Horizon. PMO 108.557–108.558 comes from a level 0·5–1·0 m above the *Ceratopyge* Limestone, and belongs to the 'earliest dichograptid fauna' *sensu* Tjernvik (1956). SGU Type 5468 is associated with a typical *T. phyllograptoides* Zone fauna. Both specimens are preserved in low relief in dark shale.

Description. These two specimens are older than the *C. multiplex* fauna from Hunneberg. They differ from the latter species in having longer thecae, resulting in wider stipes (maximum 2·1 mm) and increased thecal overlap
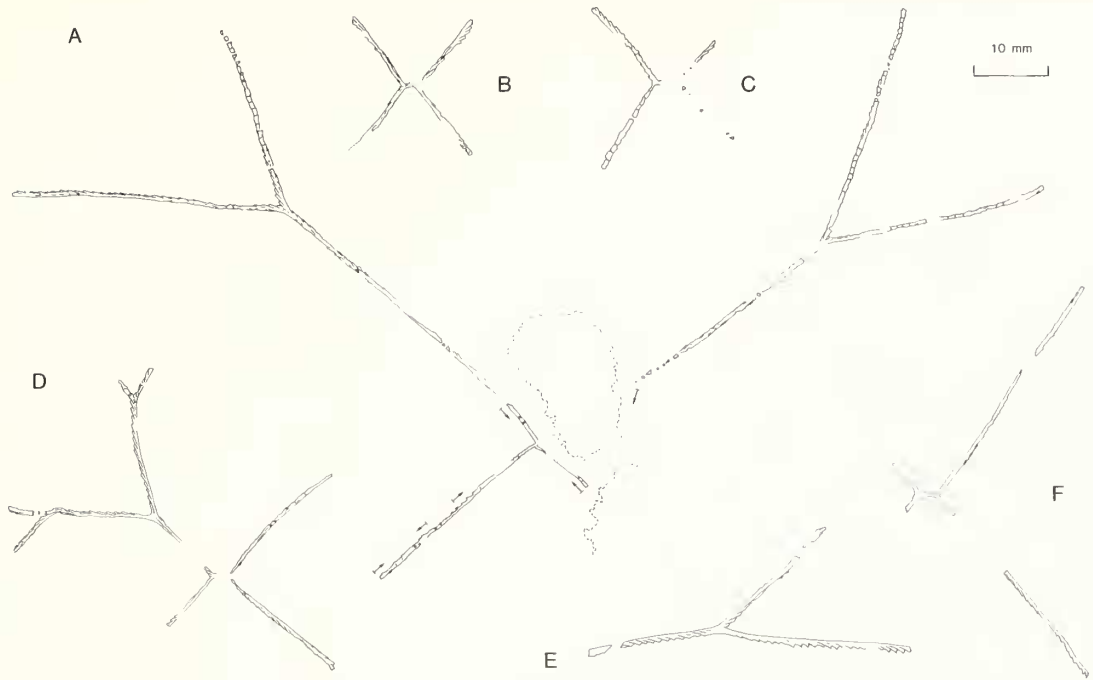
TEXT-FIG. 13. *Clonograptus* (*Clonograptus*) *galgebergi* (Monsen, 1937). A, PMO K932, the holotype, Galgeberg, Oslo; collected by Monsen. The arrows indicate the areas prepared by Lindholm. B, C, two immature specimens associated with the holotype. D, PMO K951, from Galgeberg, Olso; collected by Herrmann. E, F, LO 6057t, 6058t, from Diabasbrottet, both from 3·20 m above the lower Planilimbata Limestone band; collected by K. Lindholm.

(*c.* two-thirds). The supple stipes, consistently preserved in profile view, and the narrow proximal part, indicate little cortical overgrowth. A pyritized stipe fragment associated with PMO 108.557–108.558, and having the same branching pattern, shows remnants of a triad budding mechanism without bithecae (Pl. 83, fig. 7). SGU Type 5468 is slightly younger stratigraphically, and is too flattened to show any such details. Its dorsal margin is somewhat undulating in places, which could indicate a similar budding mechanism. The specimens have second-order branches 12–37 mm long, and stipes of all orders seen (up to the fifth) are straight or nearly so.

Discussion. The specimens are very similar to *Clonograptus* sp. A of Jackson (1974) from the uppermost Tremadoc of the Yukon. They differ only in having slightly closer spaced thecae.

Clonograptus (*Clonograptus*) *galgebergi* (Monsen, 1937)

Text-fig. 13

vp 1937   *Herrmannograptus galgebergi* n. sp. Monsen, pl. 6, fig. 5; pl. 15, fig. 10 (*non* pp. 191–192; pl. 15, fig. 3 = indeterminate fragment).
vp 1937   *Clonograptus* cf. *flexilis* (J. Hall); Monsen, pl. 6, figs. 1 and 8 (*non* pp. 195–196, pl. 6, fig. 3).

Material. The holotype, PMO K932 (Monsen 1937, pl. 6, fig. 5), associated with two immature specimens (text-fig. 13 A–C herein); PMO K951 (Monsen 1937, pl. 15, fig. 10) (text-fig. 13 D); and PMO 59.554, two fragments (Monsen 1937, pl. 6, figs. 1–8). All of these are from Galgeberg, Olso, Norway. LO 6057t and LO 6058t (text-fig. 13 E, F), from Diabasbrottet, north-west Hunneberg, Sweden; from a level approximately 1·5 m below the base of the main *C. multiplex* horizon. All specimens are in low relief and occur in dark shale.

Horizon. *T. approximatus* Zone *sensu* Monsen (1937).

Diagnosis. A clonograptid very similar to *C. multiplex*, differing mainly in having narrower stipes with straighter thecae. The available specimens have widely spaced dichotomies. There are no bithecae along the stipes.

Redescription of type material. The holotype (PMO K932; text-fig. 13a) lacks the proximal part, but according to stipe angles the specimen shows second- and third-order stipes. Additional preparation of the proximal part, which was not illustrated by Monsen (1937), has revealed the third and possibly the fourth second-order stipe. The fourth stipe seems slightly displaced, due possibly to the growth of a pyrite concretion. The complete second-order stipes are 45 and 46 mm long; third-order stipes are incomplete, with maximum length 35 mm. The angle between second-order stipes is 90° and between third-order stipes 60° and 70°. One of the two immature specimens (text-fig. 13b) associated with the holotype shows the first-order stipes, which consist of one theca each. In these specimens the angle of divergence between second-order stipes is 98–110°. Lateral stipe width is uniformly 0·5 mm, profile width 1·0 mm. Thecae are straight tubes, with length/width ratio *c.* 3. There are 9–10·5 thecae in 10 mm; thecal overlap is slightly more than half.

The other type specimen (PMO K951; text-fig. 13d) shows fourth-order stipes. First-order stipes apparently consist of one theca each, while second-order stipes are of unequal length. Complete second- and third-order stipes are shorter than those of the holotype, but the specimens agree closely in other parameters. No bithecae are visible in any specimen.

Discussion. The measurements of the Swedish specimens (text-fig. 13e, f) conform to those of the holotype, whereas the thecae are slightly more crowded, 11–12 in 10 mm, in PMO 59.554.

Our concept of this species differs from that of Monsen. She considered the main characteristic of the species to be the length of second-order stipes (Monsen 1937, p. 190), which we have proved (see description of *C. multiplex*) to be of little consequence in clonograptids. It can also be seen, from the measurements given in Monsen's original description of *H. galgebergi*, that part of her material belonged to *C. multiplex*. The available specimens do not permit any comments as to the other specific characters mentioned by Monsen, namely: a limited number of stipes; the approximately equal length of second- and third-order stipes; the constant angle of divergence; and a higher degree of regularity of the rhabdosome than the other species of '*Herrmannograptus*'.

The available material for this species is very limited, and further finds may prove it to be a subspecies of *C. multiplex*. The specimens examined differ from the latter in having narrower stipes and straighter thecae.

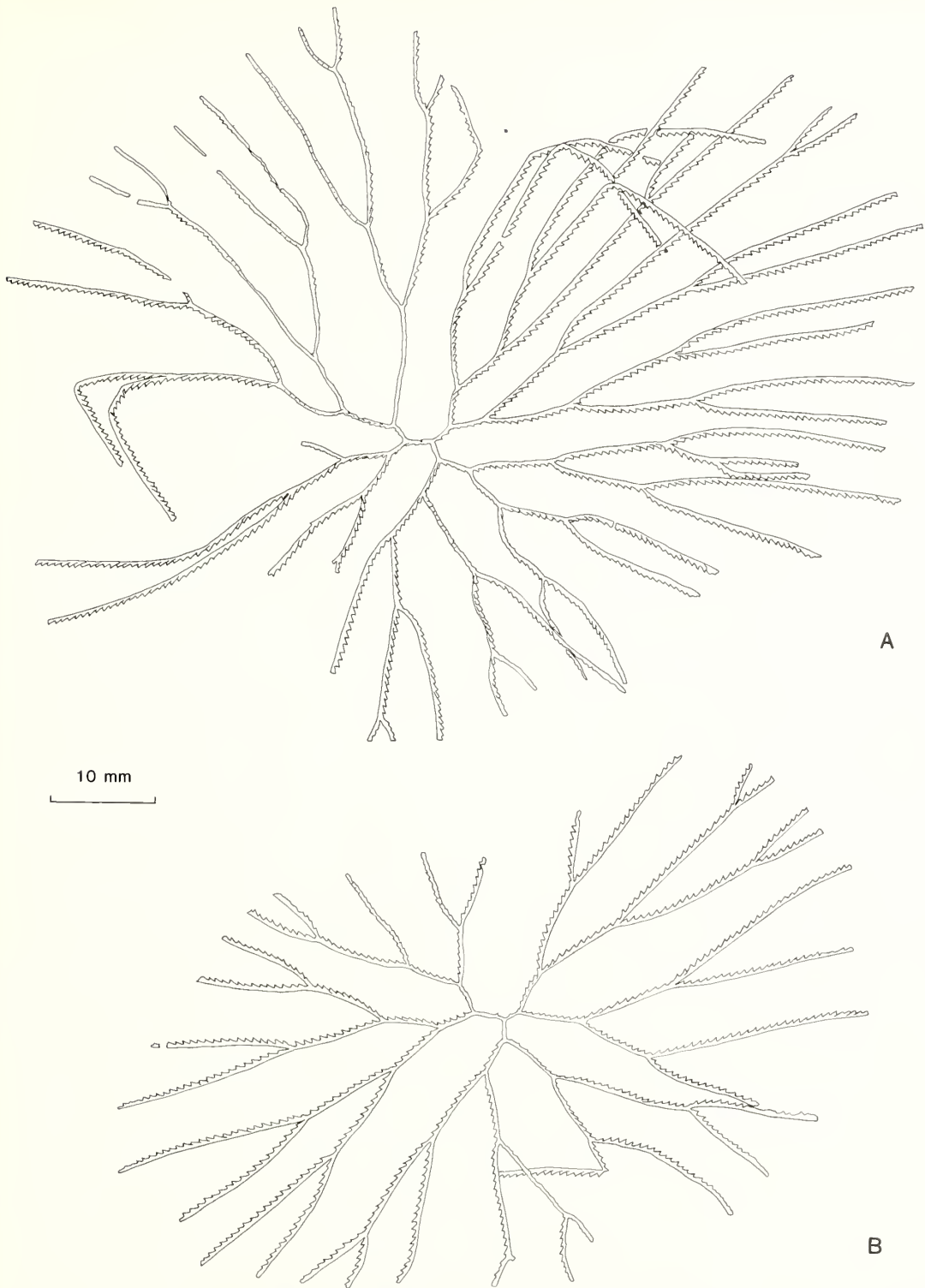## *Clonograptus* (*Clonograptus*) *milesi* (J. Hall, 1861)

Text-figs. 4a–f, 14

v 1861   *Graptolithus Milesi* n. sp. J. Hall, p. 372, pl. 12, figs. 2–4.
v 1865   *Graptolithus Milesi* J. Hall; J. Hall, p. 20, fig. 27.
v *non* 1882   *Dichograptus* (?) *Milesi* (J. Hall); Herrmann, pp. 351–352, pl. 2, figs. 17, 18.
v *non* 1937   *Herrmannograptus milesi* (J. Hall); Monsen, pp. 190–191, pl. 5, fig. 31; pl. 14, fig. 10; pl. 15, fig. 9.
non 1962   *Clonograptus milesi* (J. Hall); Obut and Sobolevskaya, p. 78, pl. 3, fig. 1.

Material. Our material consists of the specimens found on the type slab, AMNH 433/1 (i.e. the two specimens illustrated by J. Hall 1861) (text-fig. 14 herein), and fourteen associated smaller specimens on the back of the slab, some of which are illustrated as text-fig. 4a–f. They are all preserved in low to medium relief on a loose slab of greyish brown shale from Monkton, Vermont. We choose as lectotype the specimen illustrated by J. Hall (1861, pl. 12, fig. 2) (text-fig. 14a herein).

Horizon. The stratigraphic level of the type slab is unknown, since no associated fauna exists.

Diagnosis. A clonograptid of about the same size and branching density as *C. ridigus*, but with slightly narrower stipes and somewhat more closely set thecae, mostly 12–14 in 10 mm. The types present a profile view throughout the rhabdosome. No cortical thickening has been observed. There is a sicular bitheca but no bithecae along the stipes.

TEXT-FIG. 14. *Clonograptus* (*Clonograptus*) *milesi* (J. Hall, 1861), the specimens illustrated by J. Hall (1861), from Monkton, Vermont. A, AMNH 433/1-1, the lectotype. B, AMNH 433/1-2, associated with the lectotype. The orientation of the specimens on the slab is such that the thecae of both specimens point in the same direction.

Redescription of type material. The small specimens associated with the types reveal some previously unknown details. The sicula is 1·0–1·1 mm long and 0·25–0·3 mm wide near the aperture. It is curved so as to make a more or less symmetrical pair with th1¹. A sicular bitheca is present (text-fig. 4D). The proximal development appears to be isograptid (text-fig. 4E). The thecae are almost straight tubes, expanding somewhat towards the aperture and with a distal inclination of 30–35°; thecal overlap is slightly less than half, giving a deeply indented appearance. The thecal apertures make an angle of 70–90° with the dorsal margin, the variation presumably being caused by slight tectonic distortion. The same mechanism obviously explains the variation in thecal density: c. 11·5–13 thecae in 10 mm along tension, 13–15 at right angles to this direction. The first-order stipes normally consist of two thecae each, but three and one have also been observed. The two first-order stipes are sometimes of unequal length. Throughout the rhabdosome, lateral stipe width is 0·35–0·4 mm; stipes are mostly seen in profile, when they are 0·6–0·75 mm wide. There is no noticeable cortical thickening in any specimen. There are no bithecae along the stipes.

The branching pattern, irregular branching intervals, and average stipe length are very similar to those of *C. flexilis*. Second-order stipes consist of 2–5 thecae, higher orders are greatly variable: third order 3·5–11·5 mm in the lectotype and 3·5–6·5 mm in the other type; fourth order 4·5–9·5 and 7·5–15 mm respectively; fifth order 7–31 mm in the lectotype, mostly incomplete in the other specimen; one branching to seventh order occurs in the lectotype.

The angle of the second dichotomy is 90–100° and of the third 50–95°. The great spread of the latter is probably caused by twisting of the stipes, which already show thecae in profile view by the second or third order. All thecae in both types face the same direction (see text-fig. 14), and the types are oriented on the slab so that all thecae face the same way, suggesting a feature of burial.

Discussion. C. milesi shares some important features with *C. rigidus*: the prolonged first-order stipes, the short sicula (that of *C. flexilis* is almost twice as long), and the narrow stipes, but it is of somewhat smaller dimensions than the latter. It is probably the closest relative to *C. rigidus* among all *Clonograptus* species described so far.

Since the original publication of *C. milesi* (J. Hall 1861) is difficult to obtain, and because only a proximal detail of unknown magnification was illustrated by Hall (1865, fig. 27), there has been much confusion concerning the identity of the taxon. Actually, the species seems in all later instances to have been misidentified: no unequivocal material except the type slab exists to our knowledge. Could this be due to an unusual mode of preservation (see p. 716)?

Herrmann (1882) described *Dichograptus (?) Milesi* from Norway, based on Hall's illustration (1865, fig. 27). He did not have access to the original description (Hall 1861) and his material is conspecific with *C. multiplex*. Monsen (1937) used Herrmann's initial (1882) concept of *D. (?) Milesi* even though he later changed his mind and, quite correctly, called the same specimens *C. multiplex* (Herrmann 1886). Obut and Sobolevskaya (1962) were also unaware of Hall's original description, and used that given by Monsen (1937). However, the Russian species is not *C. multiplex*, judging by the description of the thecae. The description by Monsen (1937) was unfortunately reproduced by Ruedemann (1947), along with an illustration of *G. Milesi* from Hall's original publication.

OTHER SPECIES

A number of additional species, most of which we have not been able to study, appear from description or illustration to belong to *Clonograptus (Clonograptus)* = *Clonograptus s.s.* These are arranged below in decreasing order of certainty. Only species belonging to the subgenus, or those likely to do so on better description, are mentioned. We have not considered possible synonymies among these species.

Clonograptus (Clonograptus) *species*

(a) Species resembling *C. (C.) rigidus* are *C. (C.) yushanensis* (Chen *in* Chen *et al.*, 1983) and *C. (C.) utahensis* (Braithwaite, 1976). *C. yushanensis* is a narrow form with straight thecae. Its lateral stipe width varies from 0·3 to 0·6 mm; the profile width is slightly less than 1 mm as seen in the illustration, and the branching intervals are rather close to those of *C. rigidus*. Braithwaite's (1976, pl. 4, fig. 15) illustration of the holotype of *C. utahensis* shows the two counterparts arranged in a misleading manner – superficially they appear to constitute one specimen with very long first-order stipes. His other figured specimens show first-order stipes ranging from

3 to 5 thecae. The species resembles *C. rigidus* in thecal density, thecal overlap, and profile stipe width, while its branching intervals resemble *C. multiplex* more closely.

(b) Species resembling *C. (C.) flexilis* are *C. (C.) trochograptoides* (Harris and Thomas, 1939) and *C. (C.) persistens* (Harris and Thomas, 1939). Both species originate from the Bendigonian of Victoria. They both have thecae of normal *Clonograptus s.s.* appearance, and also a mode of branching compatible with *C. flexilis*. *C. trochograptoides* is a very densely branching and heavily cortexed form, with at least eleven orders of branching (Cooper 1985); *C. persistens* may possibly have two thecae on each first-order stipe, like *C. rigidus* and *C. milesi*.

We have studied *Clonograptus* sp. of Cooper (1979, pl. 2, fig. f) and found the specimen to be very similar to *C. flexilis*, differing only in having broader stipes, up to 2·1 mm. It is the youngest *Clonograptus s.s.* species we have encountered, and is from the mid-Arenig *Isograptus victoriae lunatus* Zone in New Zealand.

(c) Species more closely allied to *C. (C.) multiplex* are: *C. (C.) magnificus* (Pritchard, 1892); *C. (C.)* sp. A (Jackson, 1974); *C. (C.)* spp. B and C (Kraft and Mergl, 1979); '*Tennograptus* aff. *regularis*' Cooper, 1979; and probably the *C.* sp of Gutierrez Marco (1982, text-fig. 2j) = '*Clonograptus (Herrmannograptus)* cf. *milesi*' of Gutierrez Marco (1986, pl. 9, figs. 1–3).

The second and third of these species are discussed above in connection with *C.* aff. *multiplex* and *C. multiplex*, respectively. *C.* sp. C of Kraft and Mergl occurs with, and strongly resembles, their *C.* sp. B, except for its very high thecal density of 14–15 thecae in 10 mm. One of their illustrations of *C.* sp. C (1979, pl. 2, fig. 5) shows a 'trichotomy'.

C. (C.) magnificus is currently being studied by Gwynne Morris (Cambridge). It occurs in the Lancefieldian 2 of Victoria (Pritchard 1892) and corresponding beds of New Zealand (Benson and Keble 1935). It is undoubtedly the largest species of *Clonograptus s.s.*, reaching a maximum diameter of at least 1 metre. Apart from the gigantic final size there are no fundamental differences between it and *C. multiplex*. A few of the Swedish *C. multiplex* specimens (see text-figs. 8E, 9E, and 10D) have second-order stipes of almost the same length as that of Pritchard's (1892) specimen. The final size of *C. multiplex* is unknown, since even our largest specimens are incomplete.

'*Tennograptus* aff. *regularis*' of Cooper (1979) comes from the *Adelograptus* Zone of New Zealand and is named from Törnquist's (1904) species '*Dichograptus regularis*', which we synonymize above with *C. multiplex*. The specimen is closely similar to our Swedish *C. multiplex* fauna. It has 10·5 thecae in 10 mm, the thecae are apparently of *C. multiplex* type, the stipe width is 1·3 mm, and stipe lengths and branching angles are normal for *C. multiplex*. Our only reason for not synonymizing the New Zealand specimen with *C. multiplex* is its greater age, as shown by the associated species. This may be a parallel case to *C.* aff. *multiplex* described above, i.e. the persistence of anisograptid characters, but here impossible to detect due to flattening.

C. cf. *milesi sensu* Gutierrez Marco has very little cortical thickening. The species has prolonged first-order stipes consisting of two or three thecae. Its stipe lengths and branching pattern strongly resemble those of *C. multiplex*. The species is reported to have 6–8 thecae in 10 mm, and a stipe width of 0·5–1·2 mm.

No bithecae have been reported in any of the above species.

Clonograptus (Clonograptus?) *species*

(a) Some Lower Arenig forms have first order stipes consisting of several thecae. The type species and *C. milesi*, and occasionally other species, have slightly prolonged first-order stipes, but the material available is insufficient to estimate the potential variability within the subgenus. We therefore assign the following two species with some doubt to *Clonograptus s.s.*: *C. (C.?)* sp. A (Kraft and Mergl, 1979); and '*Tennograptus* sp.' of Gutierrez Marco (1982, text-fig. 2 k) = '*Clonograptus (Funiculograptus)* cf. *ramulosus*' of Gutierrez Marco (1986, pl. 10, figs. 1, 3, 6, 7).

We have seen one specimen of '*Funiculograptus*' (Gutierrez Marco 1986, pl. 10, figs. 6, 7). It has six thecae on each first-order stipe. No stipe is preserved in full profile view, but stipe width can be calculated at maximum 1·2 mm. There are 12 thecae in 10 mm. Thecae are of normal dichograptid appearance.

Both species seem most closely related to *C. multiplex*, in which the variation in first-order stipe length is apparently very limited.

(b) *Calamograptus* Clark, 1924, was included in *Holograptus* by Ruedemann (1947), whereas Bulman (1955, 1970) considered it to be the closest relative of *Tennograptus*. We propose here to treat *Calamograptus* as a synonym of *Clonograptus*, provisionally as *Clonograptus (Clonograptus?)*.

Calamograptus porrectus, the only species of the genus, derives from Lévis, Quebec, where it was found at the same horizon as *C. flexilis* and *T. approximatus*. Its mode of branching resembles that of *C. multiplex*, but

it has a very thick cortex proximally, obscuring any trace of thecae. Clark (1924) described the thecae found on a distal stipe, noting that the thecae were of apparently normal dichograptid type, slightly curved, with a high degree of overlap, and were spaced 8–8·5 in 10 mm. The distinguishing character of the genus, as given in the original diagnosis, is successively diminishing stipe lengths, but, in reality, too few specimens are known to verify this as a constant character. The comparatively long second-order stipes did, however, permit the growth of shorter higher-order stipes without causing them to crowd together.

We have not seen the types, but measurements on the original illustrations give a slightly different impression from Clark's description. He recorded lengths of 47, 35, 30, and 22 mm for second- to fifth-order stipes, respectively, with the reservation that the latter might not be complete. These figures must have been maximum lengths; our own measurements indicate 30–44 mm, 25–34 mm, and 24–26 mm for second- to fourth-order stipes, respectively. The fourth-order stipes all issue from a second-order stipe 33 mm long. The scale of the plate may not have been given correctly, since all of these measurements are shorter than Clark's values.

Post-Tremadoc Clonograptus s.l. species

The following species are referred to *Clonograptus s.l.* due to the lack of certain diagnostic characters:

(a) Thecae unknown: *C. norvegicus* Monsen, 1937 and *C.* sp. of Berry (1960, pl. 5, fig. 1). Both of these forms have much cortex which obscures thecal details in proximal and more distal parts.

(b) Proximal part unknown, dichograptid thecae, and a clonograptid branching pattern: *C. ramulus* (J. Hall, 1865); *C. noveboracensis* (Ruedemann, 1904); *C. atheniensis* (Ruedemann, 1947). The validity of these names is questionable, since all are described from stipe fragments only. *C. ramulus* has been found in the *T. approximatus* Zone at Lévis, whereas *C. noveboracensis* occurs in Lower Ordovician rocks at diverse localities from the north-eastern USA to Newfoundland. *C. atheniensis* comes from the basal part of the Athens Shale, and thus is considerably younger than all other species.

Tremadoc Clonograptus species

We have paid no particular attention to the Tremadoc species of *Clonograptus*, since bithecae can be presumed to exist along the stipes, and the species thus not be referable to *Clonograptus s.s.* However, there is at least one Upper Tremadoc species without any other bithecae than that present alongside the sicula, namely *C. aureus* Jackson, 1973, from the Yukon, Canada. The bitheca is visible in his fig. 2A. According to his description, the thecae could be of '*tenellus*' type, so we hesitate to refer it to *Clonograptus s.s.*

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